

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS.

2 FEBRUARY 1994

NUMBER 497

CHELID TURTLES OF THE AUSTRALASIAN ARCHIPELAGO: I. A NEW SPECIES OF *CHELODINA* FROM SOUTHEASTERN PAPUA NEW GUINEA

ANDERS G. J. RHODIN¹

ABSTRACT. A new species of *Chełodina* (Testudines: Pleurodira: Chelidae) is described from the Kemp Welch River drainage basin, Central Province, southeastern Papua New Guinea, where it occurs in a restricted distribution. It is endemic to Papua New Guinea and isolated from other members of the genus. It is superficially most similar to *Chełodina novaeguineae* of southwestern Papua New Guinea, but osteologically more closely related to *C. longicollis* of eastern Australia. The recently described species *Chełodina reimanni* from southeastern Irian Jaya, Indonesia, is most closely related to *C. novaeguineae*.

INTRODUCTION

The side-necked turtles of the family Chelidae (Testudines: Pleurodira) from the New Guinean region of the Australasian Archipelago remain one of the most poorly known turtle faunas of the world. The zoogeography and the diversity of the snake-necked chelid turtle genus *Chełodina* that inhabits this region of eastern Indonesia and Papua New Guinea have received some attention, but are far from fully resolved. Until the latter part of this century only two species of *Chełodina* were known from the regions north of Australia: *Chełodina novaeguineae* Boulenger, 1888 and *Chełodina siebenrocki* Werner, 1901. *Chełodina novaeguineae* was known only from southwestern Papua New Guinea and adjacent southeastern Indonesian Irian Jaya, as well as from Roti Island west of Timor in Indonesia, with *C. siebenrocki* supposedly occurring only in "Deutsch-Neu-Guinea," the former German colony comprising the northern half of present-day Papua New Guinea. In 1976 Rhodin and Mittermeier described the

¹ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, and Chelonian Research Foundation, Lunenburg, Massachusetts.

new species *Chelodina parkeri* from the inland grass-swamps of Lake Murray and the Aramia River of southwestern Papua New Guinea. They also redescribed and clarified the distributional status of *C. siebenrocki*, which is endemic to the estuarine swamps of the southern trans-Fly region of southwestern coastal Papua New Guinea and adjacent southeastern Irian Jaya, and absent from the northern half of Papua New Guinea, where the type specimen had allegedly been collected. Subsequently, Philippen and Grossman (1990) described *Chelodina reimanni* from the coastal regions near Merauke, southeastern Irian Jaya, but did not compare their new species to the very closely related *C. novaeguineae* and provided no osteological description. Both *C. reimanni* and *C. novaeguineae* belong to the subgeneric group of *Chelodina* species that have relatively narrower heads, shorter necks, and broader plastrons designated as *Chelodina* spp. "A" (Goode, 1967; Burbidge *et al.*, 1974; Legler, 1985). Conversely, *C. parkeri* and *C. siebenrocki* are both members of the subgeneric group with relatively broader heads, longer necks, and narrower plastrons designated as *Chelodina* spp. "B".

Very little other work has appeared on the taxonomy or natural history of New Guinean and Australasian *Chelodina*. Gaffney (1977) performed a phylogenetic analysis of all Chelidae based primarily on cranial osteology and included some New Guinean taxa. Cann (1978) contributed a photographic documentary of some of the species, and Rhodin and McCord (1990) documented some reproductive parameters of *Chelodina siebenrocki*. Wells and Wellington (1985) created a host of destabilizing nomenclatorial novelties in their contentious catalogue of Australian reptiles, which has been severely criticized by the International Commission on Zoological Nomenclature (ICZN, 1991). In addition, very little research has been done on the New Guinean short-necked chelid genera *Emydura* and *Elseya*. In particular, McDowell's (1983) recent work is not generally accepted because of its sweeping synonymies (King and Burke, 1989), and Legler and Cann (1980) restricted their work to continental Australian taxa.

Over the last 20 years, I have been privileged in having access to the large Papua New Guinean chelid turtle collections obtained by Fred Parker and deposited at the Museum of Comparative Zoology by Ernest E. Williams. Early analysis of this material has

led to the description of *Chelodina parkeri* and redescription of *C. siebenrocki* (Rhodin and Mittermeier, 1976). Continued study of these collections has subsequently been combined with extensive comparative analysis of specimens obtained from other museums and professional colleagues as well as from personal collecting trips to Papua New Guinea and Indonesia. To date, I have been able to examine personally approximately 700 chelid turtles from the eastern Indonesian and New Guinean regions of the Australasian Archipelago, and 450 specimens from continental Australia, for a total database of about 1,150 Australasian Chelidae. Through this study, I have reached several taxonomic conclusions regarding the chelid taxa of the Australasian Archipelago. In this, the first in a series of papers documenting these conclusions, I describe a remarkable new species of *Chelodina* from southeastern Papua New Guinea. In addition, I provide the first osteological description of *C. reimanni*, and compare both these species with *C. novaeguineae* and *C. longicollis*.

In 1985, through the courtesy of Dr. Peter C. H. Pritchard, I received two specimens of what had been assumed to be *Chelodina novaeguineae* from the vicinity of Hula, Kemp Welch River drainage, 90 km southeast of Port Moresby, southeastern coastal Papua New Guinea. These two specimens would have represented an enormous range extension for *C. novaeguineae*, which occurs primarily in the Western Province of southwestern Papua New Guinea, southeastern Irian Jaya, and northeastern Australia. The Kemp Welch population is disjunct and separated from the regular range of *C. novaeguineae* by about 500 km of relatively well-collected coastal territory including the whole developed Port Moresby region. From a preliminary examination of Pritchard's two specimens I was convinced that they represented a new and distinct species. In 1987 I traveled to Papua New Guinea's Kemp Welch River area and succeeded in obtaining a third specimen of the same taxon at Bore, Kemp Welch River. In addition, I was able to examine a fourth specimen preserved in the Papua New Guinea Museum without locality data other than "near Port Moresby". Later, through the courtesy of Dr. William P. McCord I had the fortunate opportunity to examine an additional large series of 39 live specimens obtained from just east of Bore in the Kemp Welch River area, for a total study sample of 43 animals.

These 43 Kemp Welch River specimens were then compared to a series of 51 *C. novaeguineae* from southwestern Papua New Guinea, 10 *C. novaeguineae* from northern Australia, 54 *C. longicollis* from eastern Australia, 12 *C. reimanni* from southeastern Irian Jaya, Indonesia, and 7 *C. steindachneri* from western Australia, for a total study series of 177 specimens. Analysis of external morphology and cranial osteology demonstrated that the isolated Kemp Welch population of *Chelodina* was an undescribed species. It is much more closely related to *C. longicollis* of Australia than it is to either New Guinean or Australian populations of *C. novaeguineae*. I now describe this new species and name it after Dr. Pritchard, who obtained the first two specimens and brought them to my attention.

TAXONOMY

Chelodina pritchardi, sp. nov.
(Figs. 1–3 and Table 1)

Holotype. MCZ 173543, alcohol-preserved sub-adult male of 129.5 carapace length, purchased from native villagers by Anders G. J. Rhodin on 14 August 1987 at Bore, Kemp Welch River, 13 km southeast of Kwikila, Central Province, Papua New Guinea (9°53'S, 147°46'E); specimen is also former AGJR-T 1259 and bears old tags RZ Field-13602 and AMNH 133079.

Paratypes. MCZ 175813 (former PCHP 1343) and AMNH 139735 (former PCHP 1342), obtained from natives by Peter C. H. Pritchard at Port Moresby in 1978, said to be from vicinity of Hula, Kemp Welch River drainage basin, 32 km south of Kwikila, Central Province, Papua New Guinea (10°06'S, 147°43'E).

Referred Specimens. PNGM 23373, collected by natives “near Port Moresby” (possibly in Kemp Welch River drainage basin), Central Province, Papua New Guinea, died in captivity at Moitaka Zoo, Port Moresby; AGJR-T 1575–1609, 1643–6, ca. 10 km east of Bore, Kemp Welch River region, Central Province, Papua New Guinea (39 specimens from Dr. William P. McCord’s private live collection, photographed and measured by Rhodin, 13 of these (AGJR-T 1601–9, 1643–6) preserved in Rhodin’s personal collection, others (AGJR-T 1575–1600) recorded in Rhodin’s turtle database; all preserved specimens eventually to be deposited in the MCZ or other museum collections).

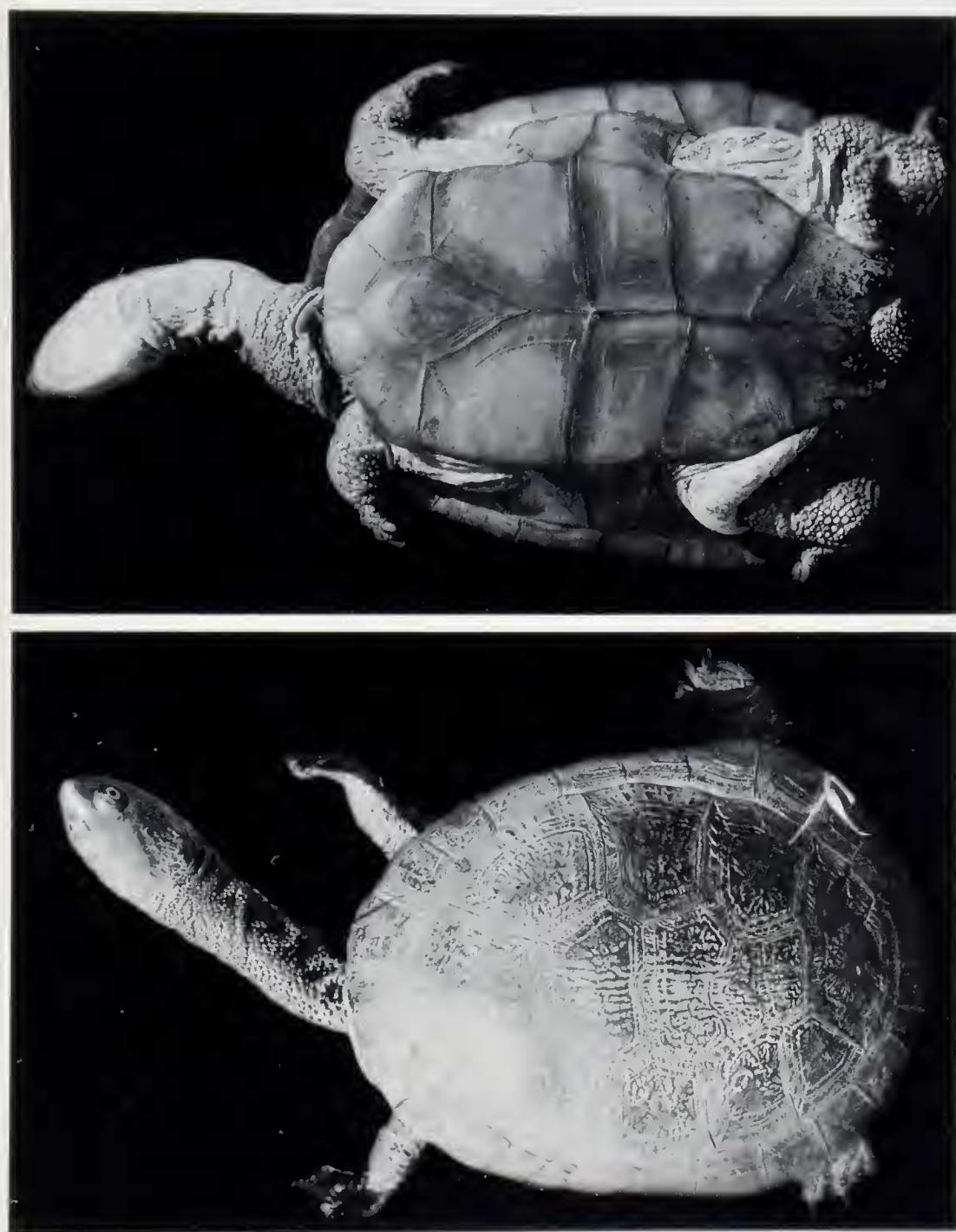


Figure 1. Dorsal and ventral views of Holotype of *Chelodina pritchardi* (MCZ 173543, sub-adult male measuring 129.5 mm carapace length) from Bore, Kemp Welch River, Central Province, Papua New Guinea, photographed while still alive.



Figure 2. Lateral head view of Holotype of *Chelodina pritchardi* (MCZ 173543). Note the striking light-colored iris.

Distribution. The species is known definitively only from the Kemp Welch River drainage basin southeast of Port Moresby, Central Province, Papua New Guinea, an area of relatively high rainfall and mesic lowland alluvial forests (Fig. 4). It appears to be absent from the Port Moresby region itself, an area of low rainfall and xeric savannah vegetation. It is not yet known whether the range also extends further southeast along the coast toward Cape Rodney and Abau, where appropriate wetland habitat also occurs. The species may additionally occur in the mesic lowland coastal plain northwest of Port Moresby in the Laloki River area, where reports tentatively suggest its presence.

Diagnosis. A medium-sized New Guinean snake-necked chelid turtle of *Chelodina* subgeneric group "A" (Burbidge *et al.*, 1974) with relatively narrow head and wide plastron (Fig. 5), superficially resembling *C. novaeguineae* but more closely related to Australian *C. longicollis*. Plastral and head widths intermediate between *C. novaeguineae* and *C. longicollis* (Fig. 6). Skull osteology distinctive: narrow maxillary and mandibular triturating surfaces with decreased anterior skull robusticity; decreased temporal fossa muscular volume with increased parietal roof width. Skull most similar to *C. longicollis*, markedly divergent from *C. novaeguineae* and *C. reimanni*, both of which have significantly more robust skulls. Eye unicolor light tan, pale plastron often with

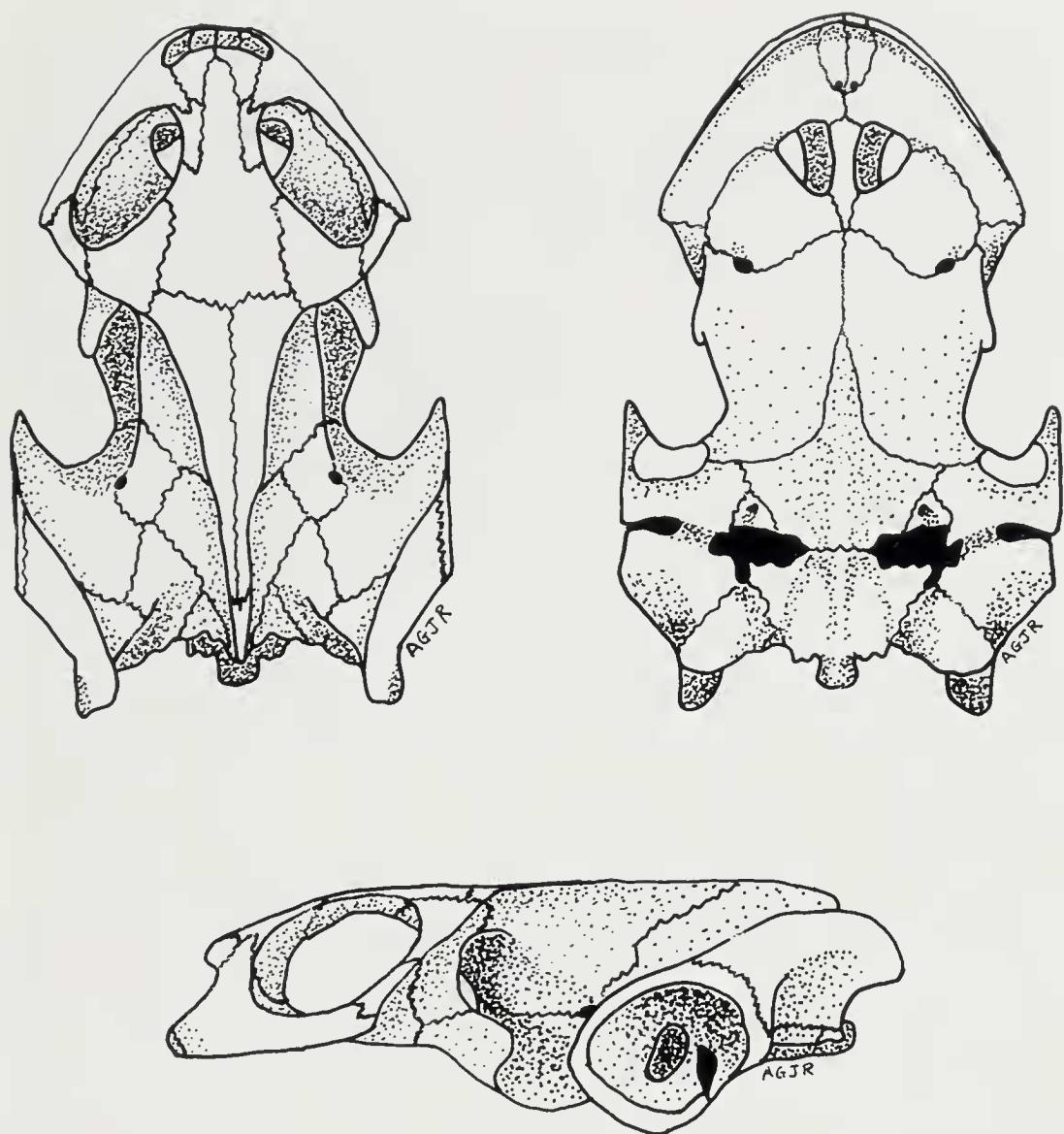


Figure 3. Dorsal, ventral, and lateral views of skull of *Chelodina pritchardi* (Paratype AMNH 139735, adult female measuring 193 mm carapace length) from nr. Hula, Kemp Welch River, Central Province, Papua New Guinea.

darker color pattern following midline sutures broadly. Eggs relatively smaller than any other *Chelodina*.

Etymology. The specific epithet is a patronym honoring Dr. Peter C. H. Pritchard, well-known turtle authority, close professional colleague, and personal friend, who serendipitously obtained the first two specimens while on a marine turtle consultancy in Papua New Guinea.

TABLE 1. BASIC EXTERNAL DIMENSIONS OF *CHELODINA PRITCHARDI*. ALL MEASUREMENTS IN MM. CL = CARAPACE LENGTH (STRAIGHT-LINE IN MIDLINE); CW = CARAPACE WIDTH (GREATEST); CD = CARAPACE DEPTH (GREATEST IN MIDLINE); PL-M = PLASTRON LENGTH (ALONG MIDLINE, NOT INCLUDING ANAL SPURS); PL-T = PLASTRON LENGTH (MAXIMUM, INCLUDING ANAL SPURS); PW = PLASTRON WIDTH (AT AXILLARY NOTCH); HW = HEAD WIDTH (TYMPANIC).

Specimen Number	Sex	CL	CW	CD	PL-M	PL-T	PW	HW
AGJR-T 1643	f	125.0	96.5	40.0	98.0	104.5	59.5	20.2
MCZ 173543	m	129.5	100.0	41.0	103.5	109.5	60.5	20.5
AGJR-T 1583	j	134.7	106.5	44.4	106.0	112.4	63.3	21.0
AGJR-T 1601	m	136.0	106.0	44.5	108.0	114.5	64.5	21.2
AGJR-T 1608	m	139.0	112.5	45.5	112.0	117.5	67.0	21.8
AGJR-T 1589	m	140.0	111.0	45.0	111.5	118.4	66.5	21.5
AGJR-T 1593	m	140.5	112.0	47.0	111.5	118.0	68.0	22.0
AGJR-T 1592	m	141.0	108.0	44.5	112.0	118.0	65.0	21.6
AGJR-T 1600	m	142.5	107.5	45.5				21.8
AGJR-T 1602	m	143.5	111.0	47.5	111.0	119.0	68.0	22.0
AGJR-T 1588	m	145.0	113.5	46.3	115.0	122.0	68.2	22.4
AGJR-T 1590	m	145.5	113.7	48.2	115.5	122.0	70.0	22.5
AGJR-T 1599	m	146.5	115.0	46.5				22.5
AGJR-T 1585	m	150.0	117.0	49.0	115.0	124.0	70.5	22.3
AGJR-T 1607	m	150.0	115.0	48.0	115.0	123.0	72.0	22.6
AGJR-T 1577	m	150.7	117.0	47.0	116.0	125.0	71.0	22.4
AGJR-T 1591	m	152.0	121.0	50.5	119.0	127.5	72.0	22.5
AGJR-T 1644	m	153.5	125.0	50.0	121.0	129.0	73.5	22.9
AGJR-T 1580	m	156.0	125.0	51.4	122.0	131.0	74.5	23.0
AGJR-T 1609	m	156.5	124.5	48.0	122.0	131.0	74.0	23.5
AGJR-T 1575	m	156.8	123.3	52.8	121.0	129.8	75.4	23.9
AGJR-T 1594	m	157.0	125.0	53.0	121.5	129.0	75.0	24.3
AGJR-T 1595	f	157.0	121.5	52.5	123.0	131.0	74.5	23.8
AGJR-T 1646	f	157.0	128.5	55.0	125.5	132.5	76.5	23.0
AGJR-T 1587	f	157.5	121.0	49.0	119.5	128.0	74.0	23.4
AGJR-T 1645	m	160.0	126.5	52.0	124.5	133.0	79.0	23.8
AGJR-T 1582	m	160.2	122.5	51.2	121.7	131.2	75.5	24.3
AGJR-T 1586	m	160.5	123.5	51.5	122.5	133.0	75.5	24.2
AGJR-T 1598	m	161.0	131.0	52.5				23.8
AGJR-T 1606	m	161.0	125.5	53.0	123.0	133.0	77.5	23.8
PNMG 23373	f	162.0	118.0	52.0	126.0		76.0	25.0
AGJR-T 1605	m	163.5	131.5	54.5	128.5	139.0	79.0	24.8
AGJR-T 1581	m	163.8	127.8	54.2	127.0	137.7	78.0	24.6
AGJR-T 1603	m	165.0	128.0	53.5	126.5	136.5	77.0	24.7
AGJR-T 1576	m	165.4	131.5	51.8	126.3	137.3	78.0	24.5
AGJR-T 1604	m	168.0	128.5	56.0	127.0	136.5	78.0	25.3
AGJR-T 1596	f	171.0	133.0	57.5				25.0

TABLE 1. Continued.

Specimen									
Number	Sex	CL	CW	CD	PL-M	PL-T	PW	HW	
AGJR-T 1597	f	175.5	138.0	59.0				25.5	
AGJR-T 1584	m	186.4	143.8	63.7	140.0	151.5	87.8	27.5	
AMNH 139735	f	193.0	156.0	62.0	154.0		93.5	27.0	
AGJR-T 1578	f	199.3	161.4	65.5	157.5	166.0	97.4	28.4	
AGJR-T 1579	f	206.0	167.0	69.5	158.0	169.0	99.0	29.0	
MCZ 175813	f	228.0	180.0	90.0	183.0		107.0	31.0	

Related Taxa. *Chelodina pritchardi* is most similar to the following four chelid taxa from New Guinea and Australia (all members of *Chelodina* subgeneric group "A").

Chelodina longicollis (Shaw, 1794). Original designation *Testudo longicollis*. Type locality "New Holland" [=Australia]. Holotype BMNH 1947.3.5.86, a dry specimen of 134 mm carapace length.

Chelodina novaeguineae Boulenger, 1888. Original designation *Chelodina novaeguineae*. Type locality "Katow, S.E. New Guinea" [= Mawatta, Binaturi River, Western Province, Papua New Guinea]. Original syntypes BMNH 1946.1.22.36 and MCG CE 8407, collected by L. M. d'Albertis. BMNH 1946.1.22.36, a subadult female of 137 mm carapace length figured by Boulenger, 1889 (plates 5, 6) and photographed in this paper (Fig. 7) is hereby confirmed as lectotype (previously designated by Wells and Wellington, 1985, p. 8).

Chelodina reimanni Philippen and Grossman, 1990. Type locality "Merauke-River, West-Irian, Neuguinea" [= Merauke River, Irian Jaya, Indonesia]. Holotype MTKD 29178, adult female of 180 mm carapace length, collected by Frank Yowono, 1988.

Chelodina steindachneri Siebenrock, 1914. Type locality "Marloo Station am Grey River in Westaustralien" [Western Australia, Australia]. Holotype NMW 19798 (Naturhistorisches Museum Wien).

DESCRIPTION

External Morphology

Carapace. Carapace of *C. pritchardi* smooth and broadly oval, width averaging 78.5% of length, moderately flared posteriorly with marginals 6–9 somewhat expanded. No lateral marginal recurving. No vertebral knobs or keel. Slight vertebral flattening or shallow furrow in some specimens. No supracaudal notch or marginal serrations. Dorsal nuchal long and broad, slightly protruding beyond anterior carapace edge in smaller specimens. Ventral un-

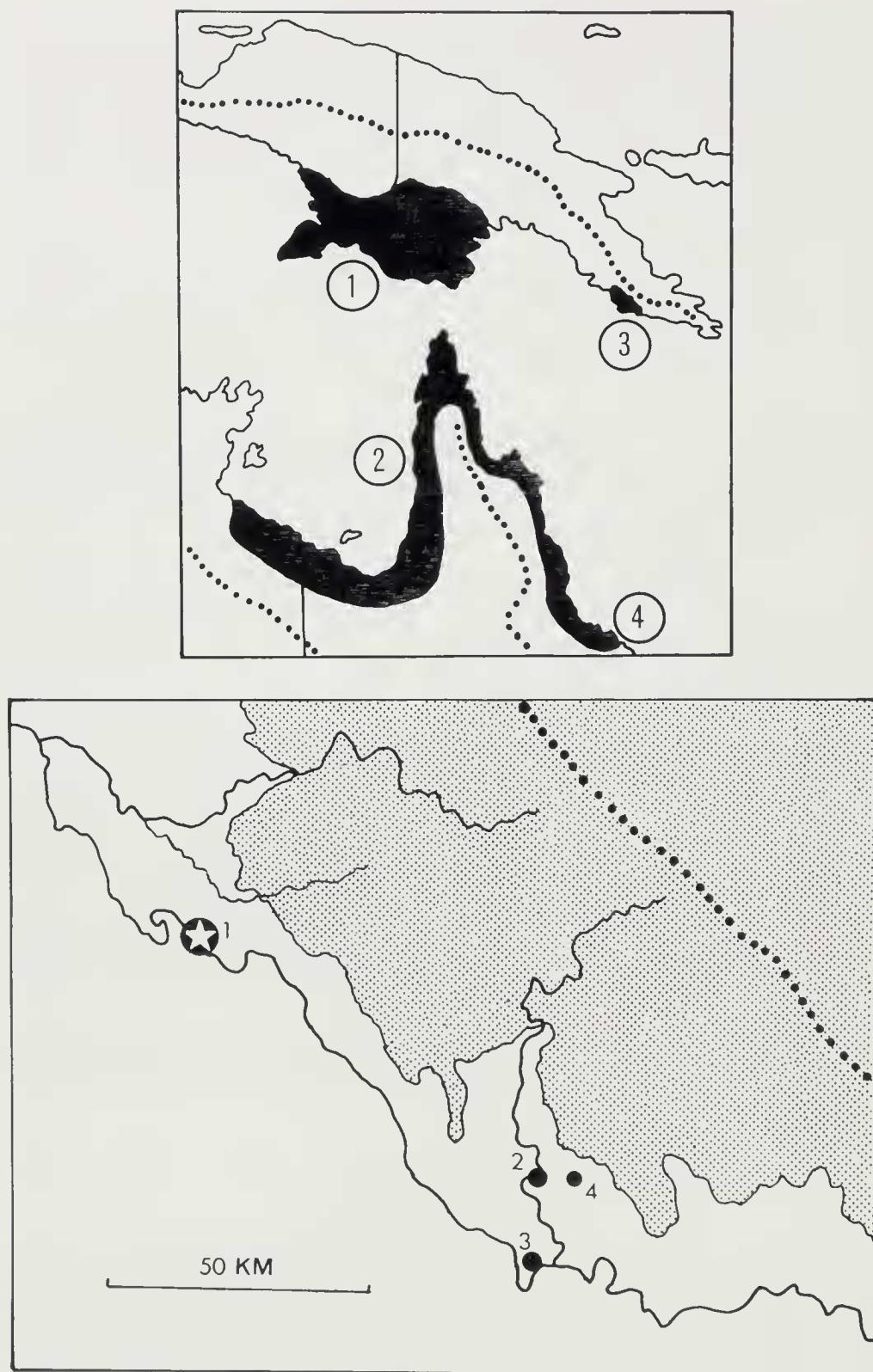


Figure 4. Top: Distribution of *Chelodina pritchardi*, *C. novaeguineae*, and *C. longicollis*. 1. New Guinean distribution of *C. novaeguineae* in Irian Jaya and Papua New Guinea. 2. Australian distribution of *C. novaeguineae* in Northern

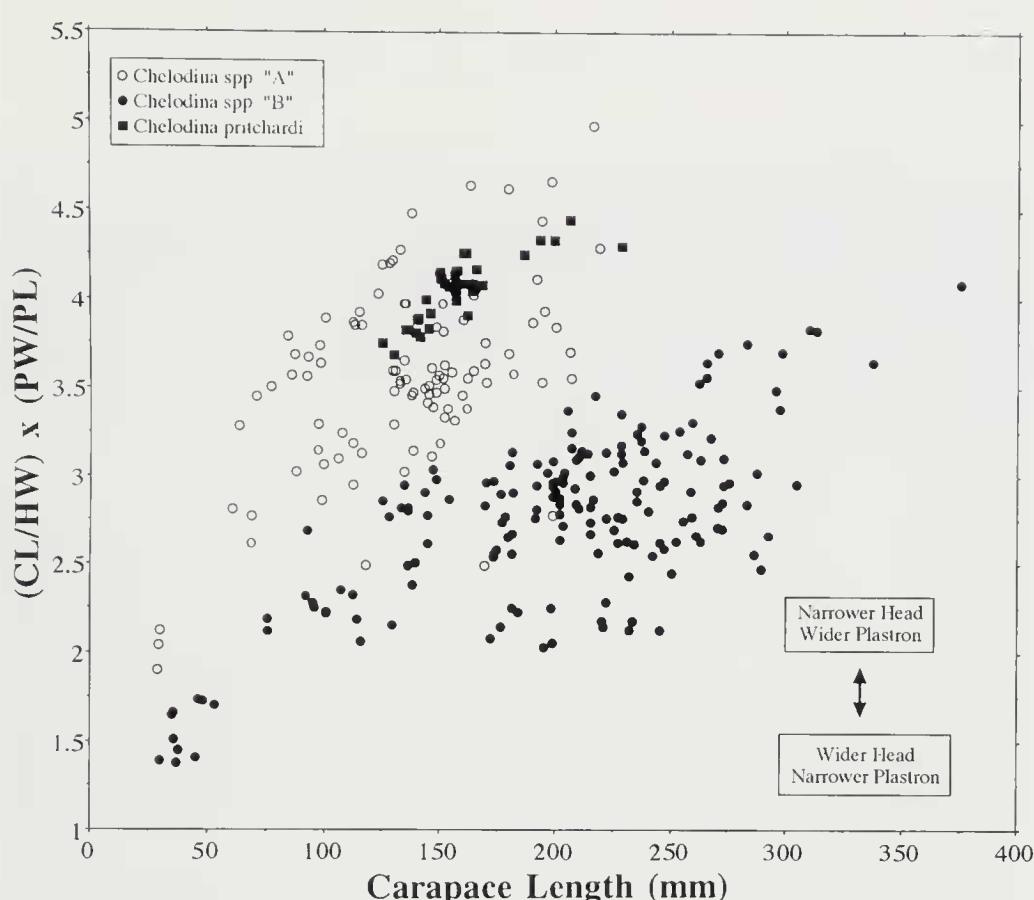


Figure 5. Scattergram plotting the relationships of head width ratio (Carapace Length/Head Width) and plastron width ratio (Plastron Width/Plastron Length), expressed as a bivariate product, versus carapace length for the subgeneric groups of *Chelodina* (*Chelodina* "A" = *C. longicollis*, *C. novaeguineae*, *C. pritchardi*, *C. steindachneri*, and *C. reimanni*, *Chelodina* "B" = *C. expansa*, *C. oblonga*, *C. parkeri*, *C. rugosa*, and *C. siebenrocki*). Note the position of *C. pritchardi* within the *Chelodina* "A" generic grouping. Note also the three specimens of subgeneric group "A" within the group "B" area; these represent extremely broad-headed *C. reimanni*.

Territory and Queensland. 3. Distribution of *C. pritchardi* in Papua New Guinea. 4. Approximate northern limit of the distribution of *C. longicollis* in eastern Australia. Major watershed limits indicated as heavy dotted lines. Bottom: Area 3 of top map enlarged here and showing distribution of *Chelodina pritchardi* in the Port Moresby region, Central Province, Papua New Guinea. The shaded area represents elevation above 200 m, the heavy dotted line shows the watershed limit of the Owen Stanley Ranges. Starred locality (1) is Port Moresby. Black dots represent localities for *C. pritchardi* in the Kemp Welch River basin, as follows: (2) Bore, Kemp Welch River; (3) Hula; (4) ca. 10 km east of Bore.

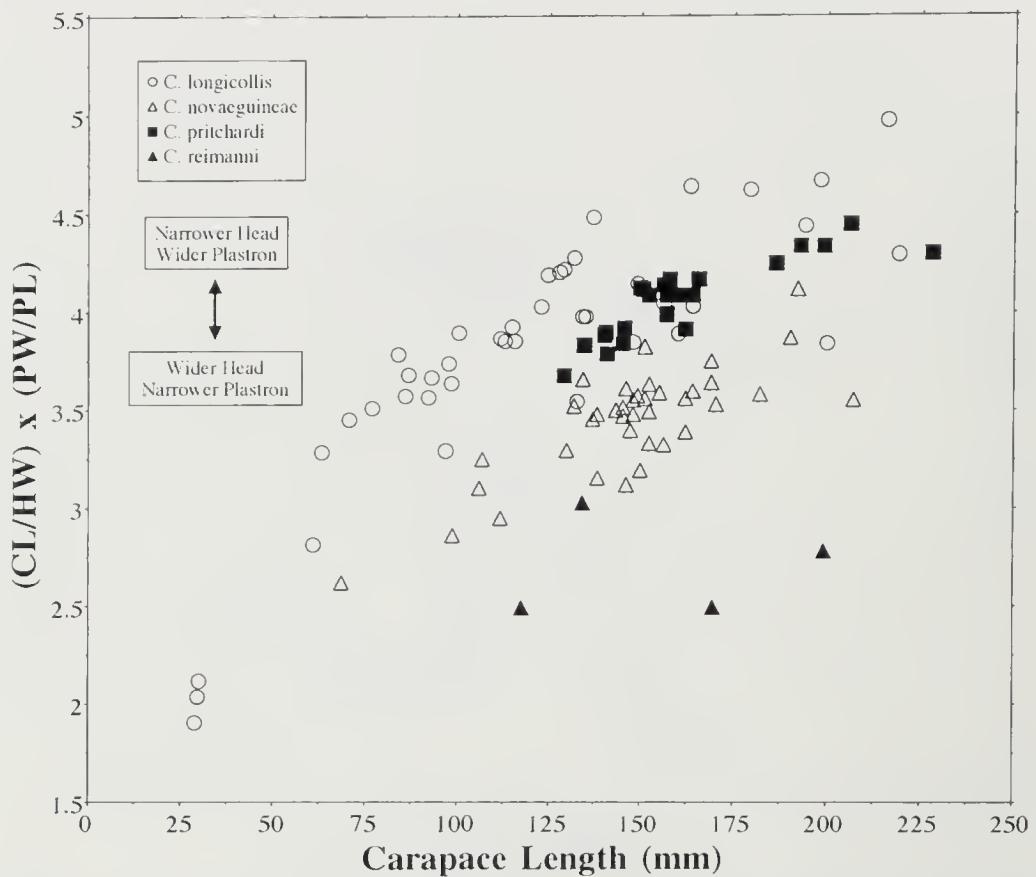


Figure 6. Scattergram plotting the relationships of head width ratio (Carapace Length/Head Width) and plastron width ratio (Plastron Width/Plastron Length), expressed as a bivariate product, versus carapace length in four species of *Chelodina*. Note that *C. pritchardi* is essentially intermediate between *C. longicollis* and *C. novaeguineae*, but more similar to *C. longicollis*.

derlap of nuchal also relatively long and broad. Vertebral 1 widest, then 2, 3, 5, and 4 in descending order of width. Carapace somewhat broader in *C. pritchardi* than in New Guinean *C. novaeguineae*, intermediate in *C. longicollis*, significantly narrower in *C. reimanni* (see Fig. 8 and Table 2).

Carapace moderately deep in older specimens, relatively flatter in younger ones. No sexual dimorphism in carapace depth in specimens examined. Carapacial scutes lightly rugose with partially retained growth lines until mid-adult size.

Color dark chestnut brown. Carapace very similar to both *C. novaeguineae* and *C. longicollis*, but generally more broad than *C. novaeguineae* and slightly less broad than *C. longicollis*. Carapace superficially more similar to *C. novaeguineae* than to *C. longicollis* (Figs. 1 and 7).

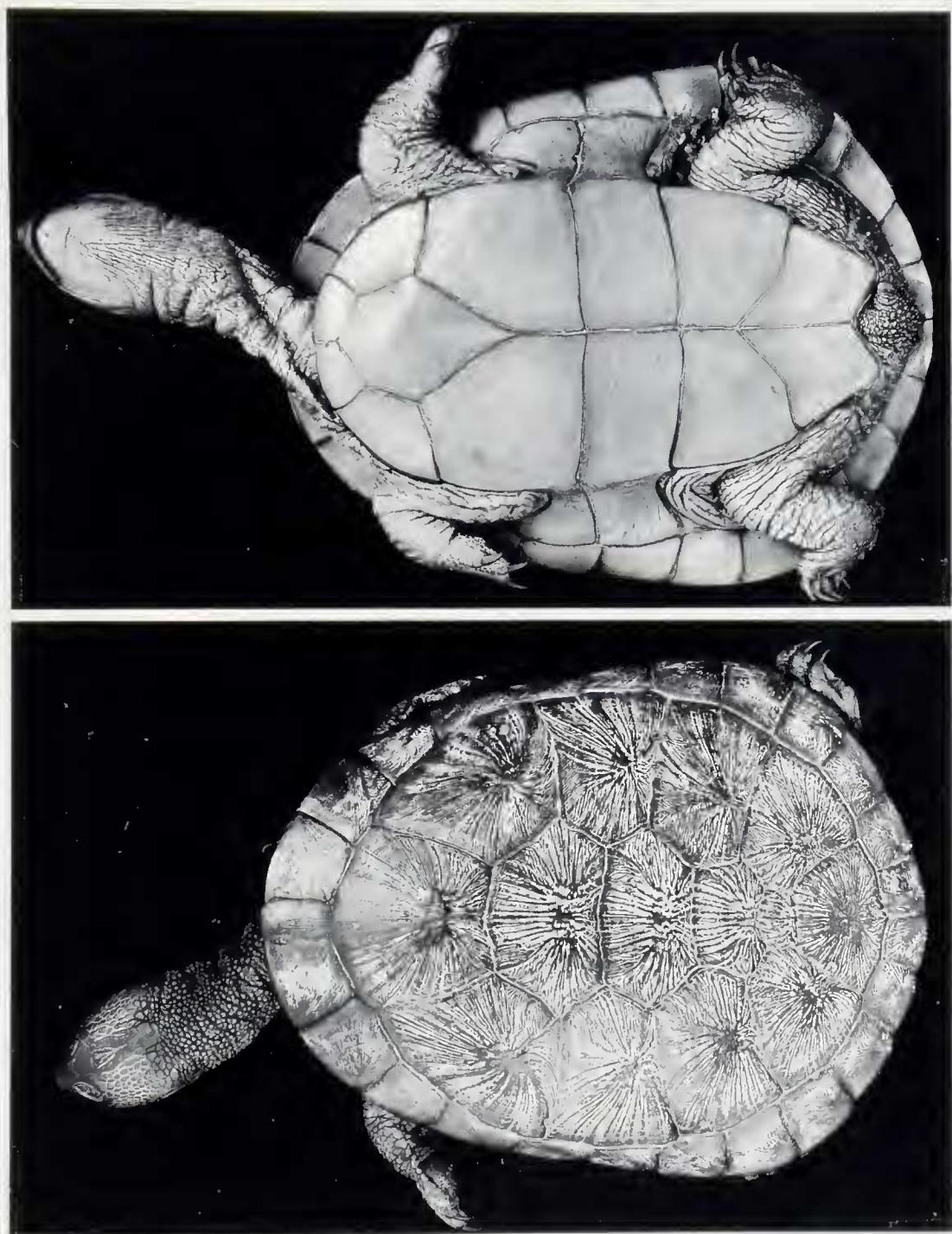


Figure 7. Lectotype of *Chełodina novaeguineae* (BMNH 1946.1.22.36, sub-adult female measuring 137 mm carapace length), from Katow, S.E. New Guinea [= Mawatta, Binaturi River, Western Province, Papua New Guinea].

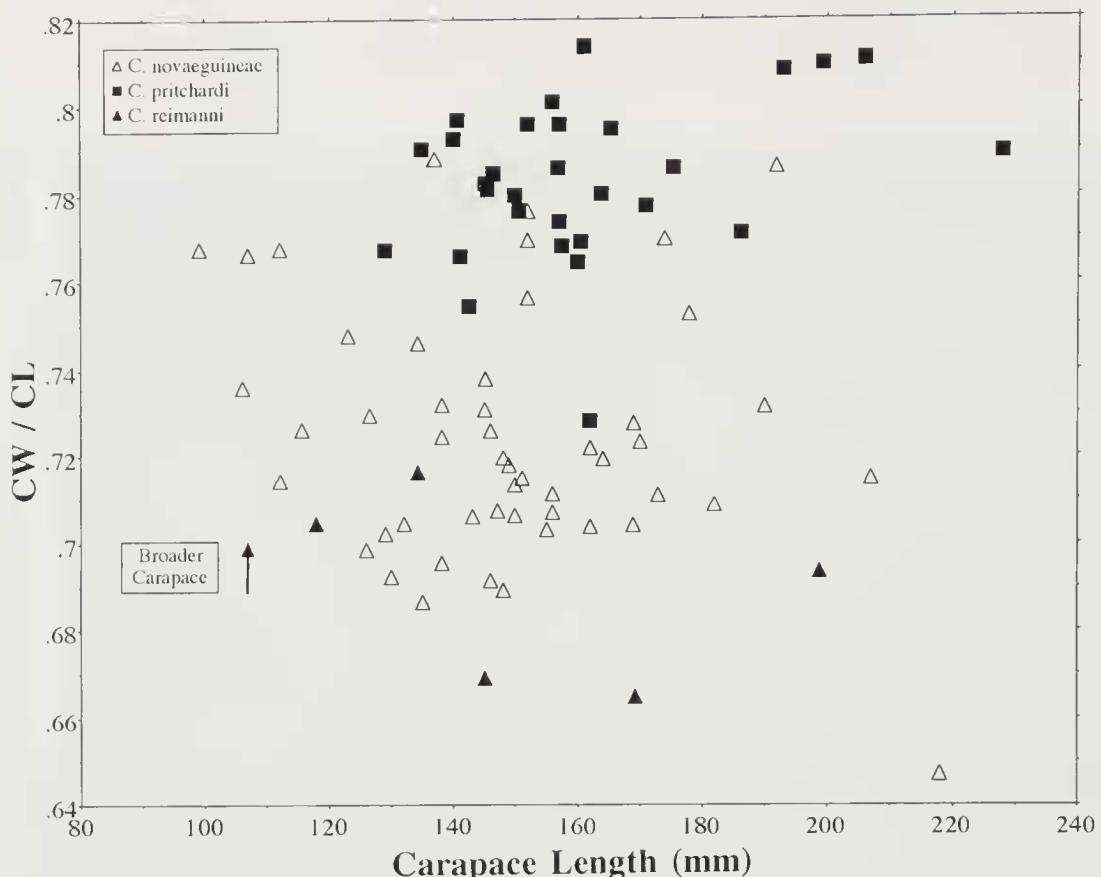


Figure 8. Scattergram plotting carapace width ratio (CW/CL) versus carapace length in three species of *Chelodina*, utilizing data only from New Guinean specimens of greater than 100 mm carapace length. Note the broader carapace in *C. pritchardi*.

Plastron. Plastron broad, axillary width averaging 61% of mid-line length, anterior lobe moderately broad, intermediate between the relatively narrow tapered lobe of *C. novaeguineae* and *C. reimanni*, and the broadly expanded anterior lobe of *C. longicollis* (Fig. 6 and Table 2). Slight secondary expansion of anterior plastral lobe at posterior border of humeral scutes, not present in *C. novaeguineae*. Anal notch moderately deep, no sexual dimorphism noted. Intergular broad, long, and recessed without marginal contact. Plastral scute suture length formula: Ig > An > Abd > Pec > Fem > Gul. No axillary or inguinal scutes.

Plastral color yellow with variable amount of light to moderate brown pigment following central portions of sutures broadly, often expanding to cover much of central plastron. Holotype plastron oxidized to darker brown. Plastral color different from *C.*

TABLE 2. MEANS AND STANDARD DEVIATIONS FOR SHELL MEASUREMENT RATIOS OF FOUR *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 1. DATA BASED ONLY ON SPECIMENS OF CARAPACE LENGTH GREATER THAN 100 MM. *C. NOVAEGUINEAE* INCLUDES ONLY NEW GUINEAN SPECIMENS, NO AUSTRALIAN ONES.

Feature	<i>C. longicollis</i> (n = 37)	<i>C. pritchardi</i> (n = 43)	<i>C. novae-</i> <i>guineae</i> (n = 51)	<i>C. reimanni</i> (n = 5)
CW/CL	.775 ± .042	.785 ± .018	.723 ± .028	.690 ± .022
PW/PL-M	.618 ± .026	.610 ± .012	.576 ± .018	.543 ± .028
HW/CL	.151 ± .012	.150 ± .005	.167 ± .010	.202 ± .012
CD/CL	.310 ± .026	.328 ± .014	.327 ± .021	.315 ± .007

novaeguineae, which usually has an immaculate yellow plastron with occasional very thin pigment lines following the sutures, and from *C. longicollis*, which usually has broad black color zones along the sutures and sometimes over most of the plastron. Plastron superficially more similar to *C. novaeguineae* than to *C. longicollis* (Figs. 1 and 7).

Head and Soft Parts. Head with small irregular scales covering temporal skin, smooth over parietal and interorbital roof. Neck with low soft tubercles, less pronounced than the larger raised firmer tubercles of *C. novaeguineae*. Soft parts grayish-brown dorsally, yellowish-white ventrally. Hands and feet with 4 claws each.

Head width narrow, typical of *Chelodina* subgeneric group "A" species (Fig. 5), intermediate between the wider heads of *C. novaeguineae* and *C. reimanni* and the narrower head of *C. longicollis* (Fig. 6). Relative width of head narrows ontogenetically.

Eye color of *C. pritchardi* primarily light tan with medium dark tan thin area at outer periphery of iris and very light tan thin inner rim, becoming nearly white along the pupillary edge of the iris. No color flecks or cross-bar. Eye color of *C. novaeguineae* from Papua New Guinea (personal observation) and Australia (Cann, 1978: plate 19) dark brown with more sharply distinct yellowish-white pupillary rim around inner iris, and dark area of iris with multiple small irregular flecks of darker and lighter pigment. Overall impression of eye color of *C. pritchardi* unicolor whitish-tan, of *C. novaeguineae* bicolor dark brown with inner yellow circle.

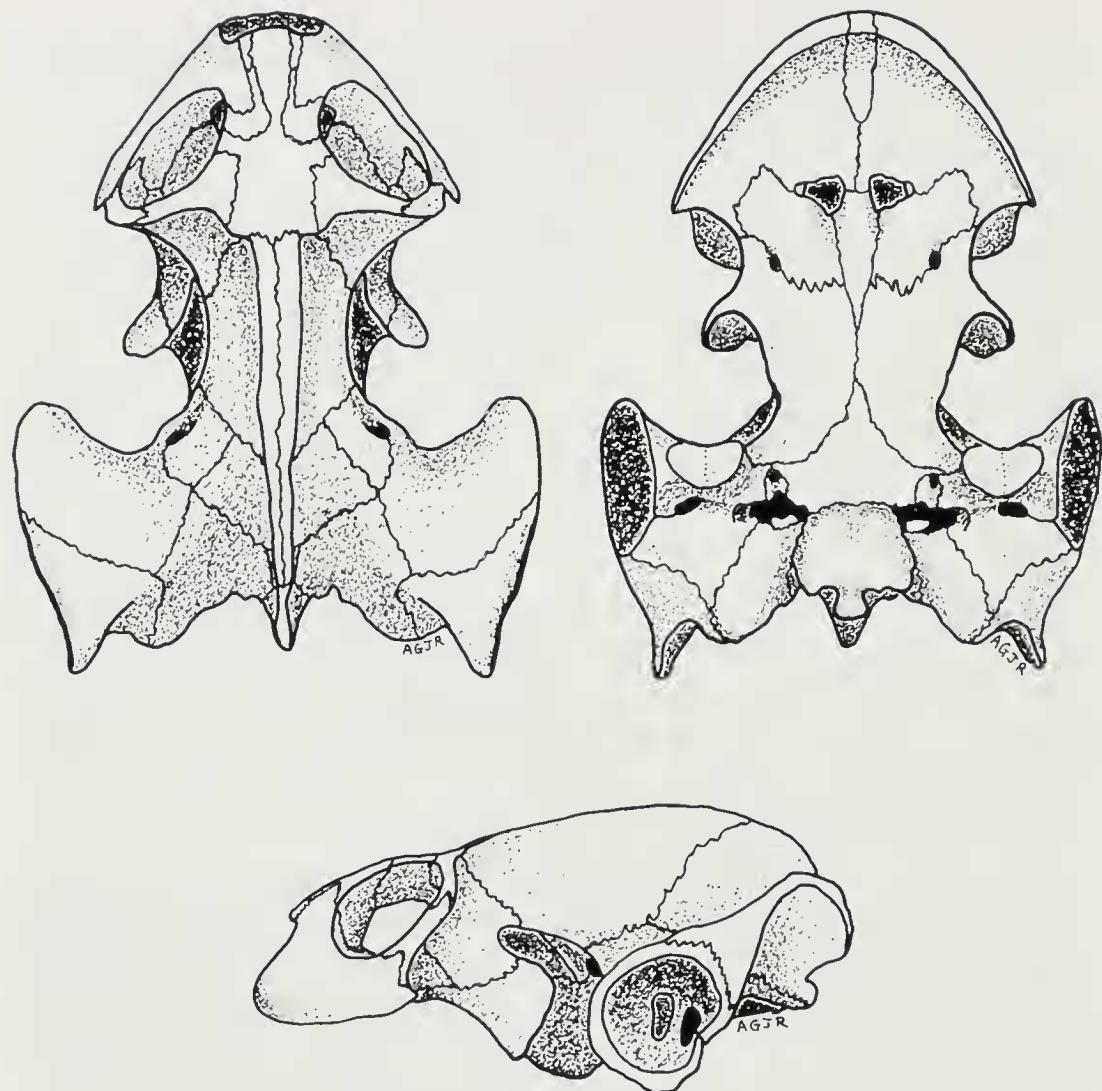


Figure 9. Dorsal, ventral, and lateral views of skull of *Chelodina reimanni* (AGJR-T 746, 199 mm carapace length female from Merauke, Irian Jaya, Indonesia).

Size and Sexual Dimorphism. The largest specimen of *C. pritchardi* recorded is a female of 228 mm carapace length. The largest male examined has a carapace length of 186 mm, indicating probable sexual dimorphism, with females larger than males. Calculating the sexual dimorphism index according to the method of Gibbons and Lovich (1990) yields an SDI value of approximately 1.22 for *C. pritchardi*. The SDI value for New Guinean *C. novaeguineae* is approximately 1.37, with the largest confirmed female measuring 207 mm and the largest male 151 mm.

The largest specimen of New Guinean *C. novaeguineae* I ex-

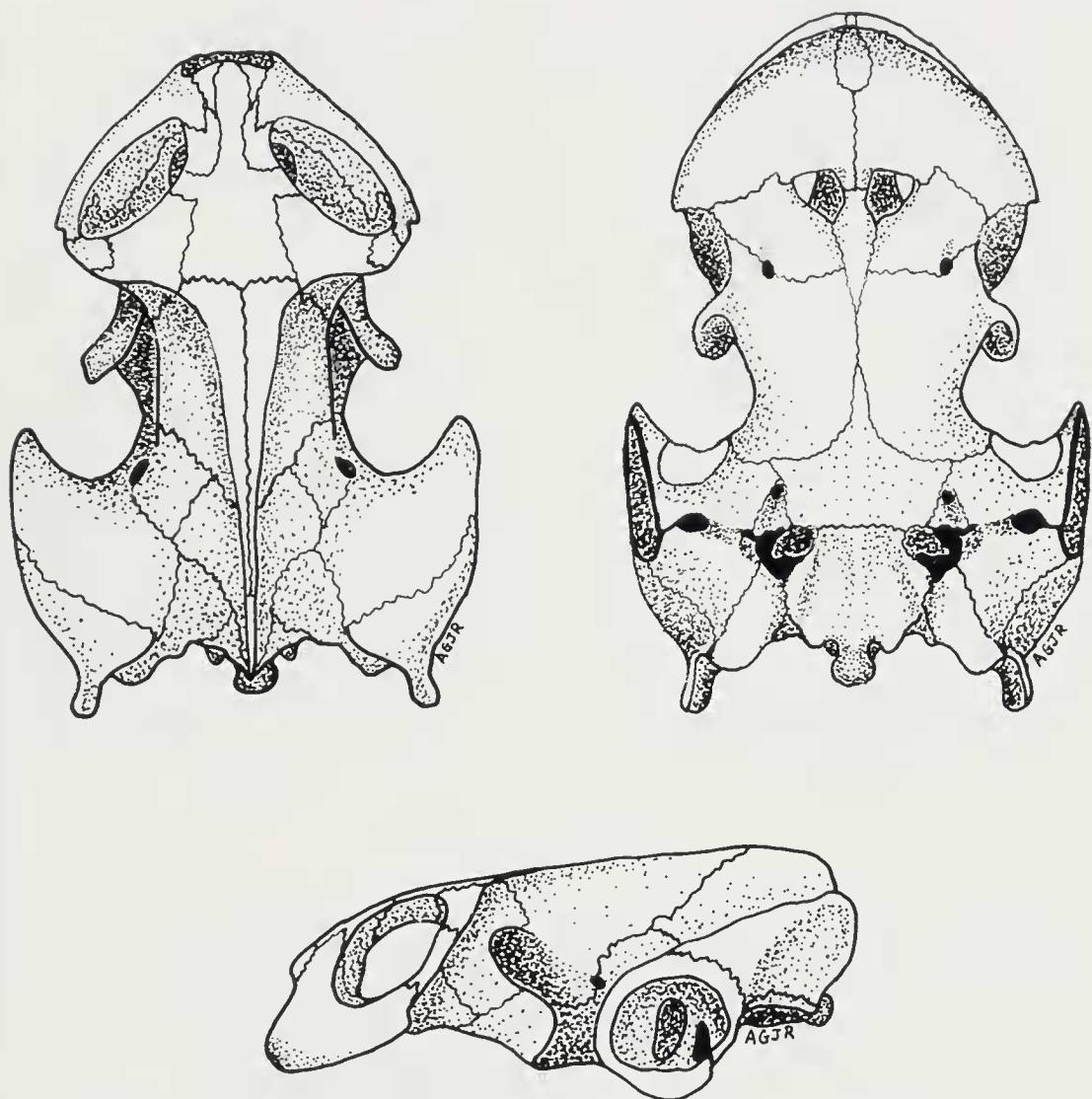


Figure 10. Dorsal, ventral, and lateral views of skull of *Chelodina novaeguineae* (AGJR-T 504, 178 mm carapace length female from Boze, Binaturi River, Western Province, Papua New Guinea).

amined was a female measuring 207 mm, but Philip Hall (personal communication) has photographed and measured a 218 mm specimen from the Irian Jaya-Papua New Guinea border. The largest specimen of Australian *C. novaeguineae* I examined measured 279 mm, but Cann (1978) records 300 mm as the maximum size. The largest specimen of *C. reimanni* I examined measured 199 mm, but Philippen and Grossman (1990) records 206 mm as the maximum size. In general, *C. pritchardi* is larger than New Guinean *C. novaeguineae* or *C. reimanni*, and smaller than Australian *C. novaeguineae*.

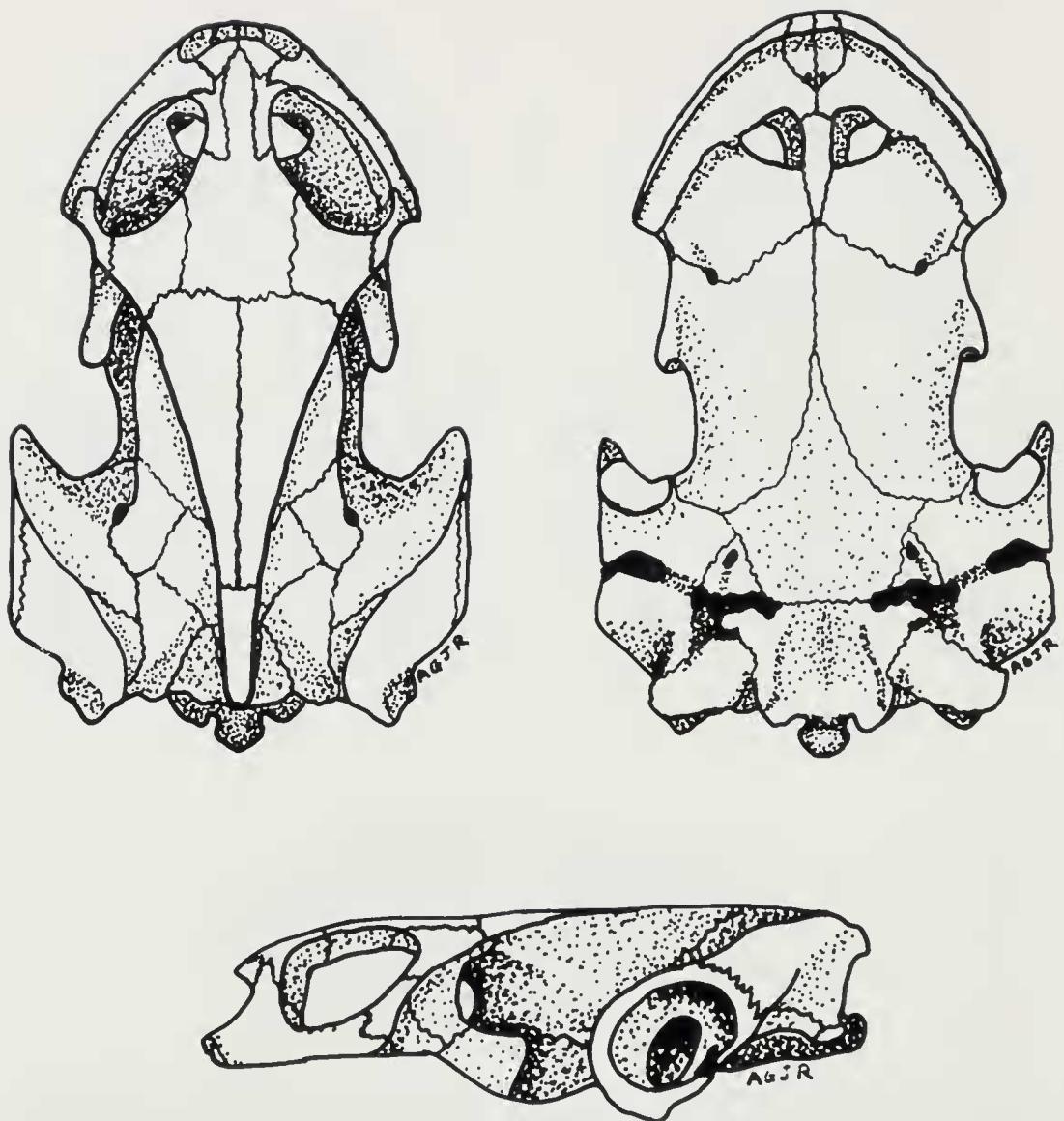


Figure 11. Dorsal, ventral, and lateral views of skull of *Chelodina longicollis* (AMNH 108952, from Patho, Victoria, Australia).

Osteology

Skull. The description of skull osteology is based on the examination of 6 skulls of *C. pritchardi*. Comparison is performed with skulls of 7 *C. longicollis*, 15 *C. novaeguineae* (12 from New Guinea, 3 from Australia), and 2 *C. reimanni*. Refer to Figures 3 and 9–11 for skull illustrations of the four species and Tables 3 and 4 and Figures 12–14 for additional skull measurements and ratios.

The skull of *C. pritchardi* is a typical *Chelodina* subgeneric group "A" type skull, not overly elongate, flattened, or wide as

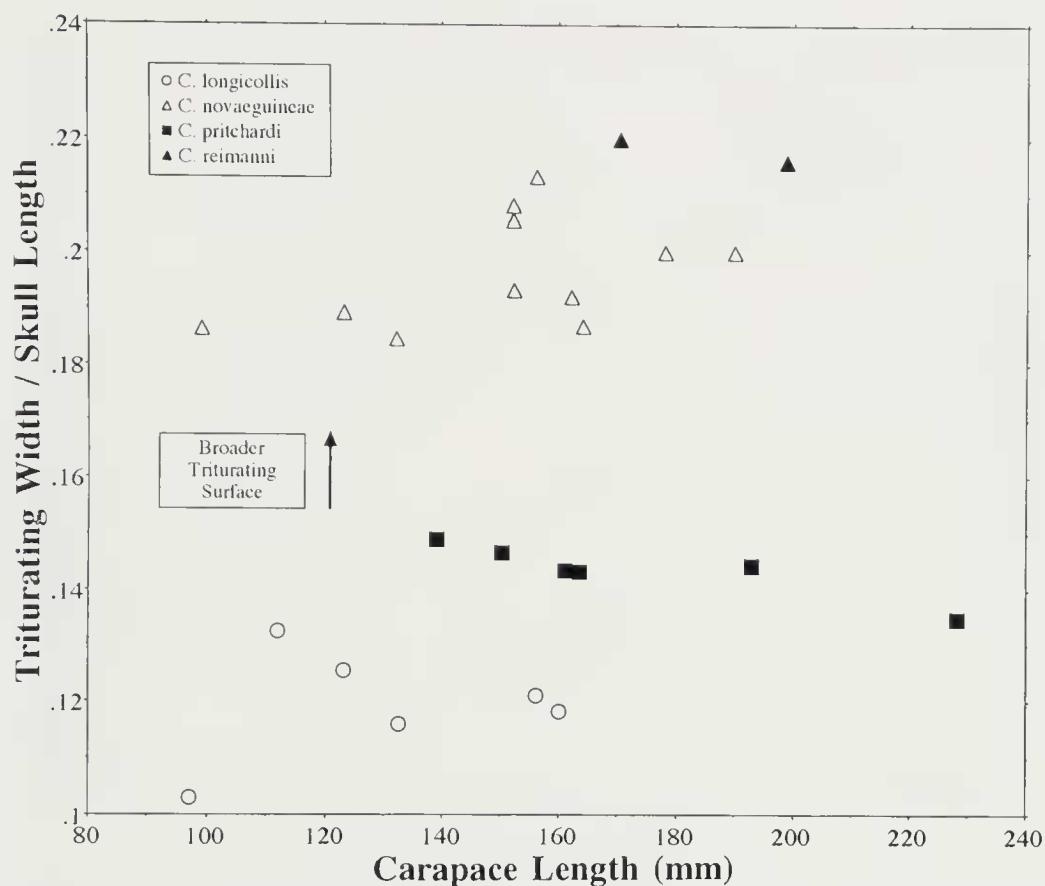


Figure 12. Scattergram plotting maxillary triturating surface width ratio (TW/SL) versus carapace length in four species of *Chelodina*. Note the much broader triturating surface in *C. novaeguineae* and *C. reimanni* with *C. pritchardi* being somewhat intermediate and *C. longicollis* much narrower.

in subgeneric group "B". It is strikingly similar to the skull of *C. longicollis*, from which it is differentiated by only a few features. It differs markedly from its more geographically proximate congener *C. novaeguineae* and *C. reimanni*.

The major differentiating features involve the width and robusticity of the triturating surfaces and the relative volume of the muscular temporal fossa. *C. novaeguineae* and *C. reimanni* have wide and robust maxillary and mandibular triturating surfaces, with correspondingly wide and robust horny rhamphothecae. *C. longicollis* has very narrow and weak surfaces and *C. pritchardi* is intermediate (Fig. 12), but more similar to *C. longicollis*. The mandibular coronoid process is high and prominent in *C. novaeguineae* and *C. reimanni*, low and less prominent in *C. longicollis*, and intermediate in *C. pritchardi*. *C. novaeguineae* and

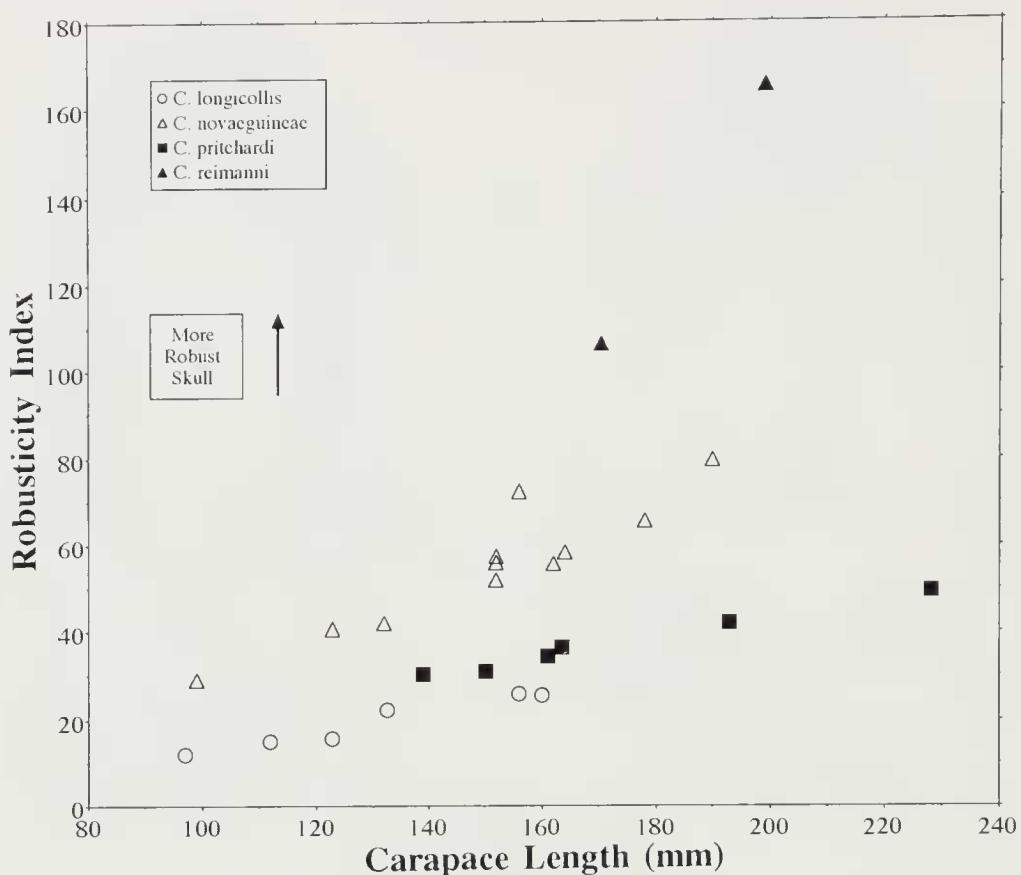


Figure 13. Scattergram plotting skull Robusticity Index [RI = (TW × SWT × SD)/SL] versus carapace length in four species of *Chelodina*. Note the intermediate position of *C. pritchardi* with reference to the other species.

C. reimanni have a long midline maxillary suture, reflecting the increased width of the maxillary triturating surface; both *C. longicollis* and *C. pritchardi* have short sutures.

The relative position of the choanae is posterior in *C. novaeguineae* and *C. reimanni*, anterior in *C. longicollis* and *C. pritchardi*, once again as a result of the widened triturating surface. The vomer is more robust, wider, and reaches further posterior in *C. novaeguineae* and *C. reimanni* than in *C. longicollis* or *C. pritchardi*. It reaches the level of the palatine foramen and separates the palatines widely in *C. novaeguineae* and *C. reimanni*, does not reach the level of the palatine foramen and only barely separates the palatines in *C. longicollis* and *C. pritchardi*. In *C. novaeguineae* and *C. reimanni* the pterygoids do not extend anteriorly along the midline to meet the vomer anterior to the palatine foramen, in *C. longicollis* and *C. pritchardi* the pterygoids do extend anteriorly.

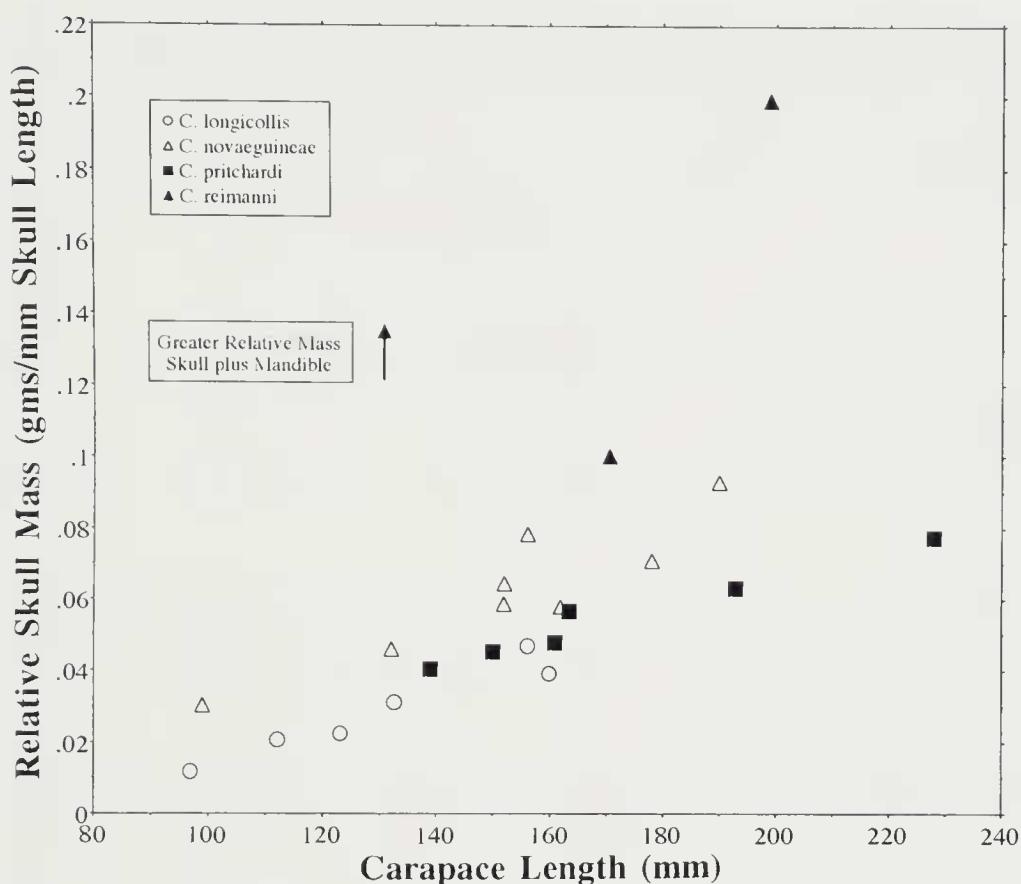


Figure 14. Scattergram plotting relative skull mass (skull and mandible weight in gms/skull length in mm) versus carapace length in four species of *Chelodina*. Note the intermediate position of *C. pritchardi* with reference to the other species, with *C. reimanni* and *C. novaeguineae* having heavier, more robust skulls.

The shape of the anterior skull tomial edge also differs, with *C. novaeguineae* and *C. reimanni* having a somewhat rounded, blunted shape, and *C. longicollis* and *C. pritchardi* slightly more angular. The premaxillae are usually fused into a single small premaxilla in New Guinean *C. novaeguineae* (11 of 12 skulls) and *C. reimanni* (2 of 2); unfused but very small in Australian *C. novaeguineae* (3 of 3), and unfused and large in *C. longicollis* and *C. pritchardi*. Premaxillary foramina are absent in New Guinean *C. novaeguineae* and *C. reimanni*, reduced but present in Australian *C. novaeguineae*, and well-developed in *C. longicollis* and *C. pritchardi*.

The ventral view of the skull reveals that the posterior extension of the quadrate beyond the posterior extension of the opisthotic differs between the species. *C. novaeguineae*, *C. reimanni*, and *C. pritchardi* have prominent quadrate extensions, *C. longicollis* does

TABLE 3. BASIC SKULL MEASUREMENTS FOR FOUR SPECIES OF CHELODINA. SL = SKULL LENGTH (SNOUT-OCCIPITAL CONDYLE); SWT = SKULL WIDTH, TYMPANIC MAXIMUM; SWM = SKULL WIDTH, MAXILLARY MAXIMUM; SDM = SKULL DEPTH AT POSTERIOR EDGE OF MAXILLAE; SD = SKULL DEPTH IN MIDLINE BETWEEN SUPRAOCIPITAL SPINE AND BASISPHENOID; IOW = INTER-ORBITAL WIDTH, MINIMAL; OW = ORBITAL WIDTH, SHORT AXIS; PtW = PTERYGOID WIDTH, MINIMAL; TW = TRITURATING WIDTH, MAXILLARY (MEASURED IN MIDLINE FROM TOMIAL EDGE TO ANTERIOR CHOANAL BORDER). REFER TO TABLE 4 AND FIGURES 12 AND 13 FOR ANALYSIS OF SKULL MEASUREMENT RATIOS.

Species		Mus. Sp. No.	SL	SWT	SWM	SDM	SD	IOW	OW	PtW	TW
<i>Chelodina longicollis</i>											
AGJR-T 159		25.2	16.1	12.8	5.9	7.1	2.4	6.0	8.8	2.6	
MCZ 8369		26.4	16.8	12.4	5.0	6.7	2.5	5.5	8.7	3.5	
MCZ 8377		27.1	17.9	13.0	6.0	7.0	2.4	5.8	9.4	3.4	
AGJR-T 158		33.6	21.6	17.0	7.3	8.9	3.4	7.0	11.1	3.9	
MCZ 86783		35.5	23.4	18.6	7.6	9.2	3.5	7.5	11.0	4.2	
AGJR-T 179		36.3	23.2	18.9	8.2	9.2	4.3	7.8	12.0	4.4	
AMNH 108952		40.5	25.1	20.2	8.2	10.1	3.5	8.3	13.9	4.6	
<i>Chelodina novaeguineae</i>											
MCZ 134394		26.3	17.8	13.3	6.6	8.8	3.0	6.3	8.4	4.9	
AMNH 57589		31.2	21.0	16.3	8.0	10.3	3.6	7.5	9.7	5.9	
MCZ 134712		32.5	22.4	16.5	7.7	10.2	3.8	7.3	10.5	6.0	
UU 14716		33.7	23.0	18.2	7.2	9.5			11.2	6.3	
MCZ 134391		35.0	23.3	17.7	8.2	11.7	4.6	7.0	10.5	7.2	
AMNH 117939		35.7		18.5		11.5	4.3	7.5	11.2	6.9	
MCZ 134395		35.7	24.0	18.0	9.0	11.2	4.7	7.8	11.8	6.9	
MCZ 134390		36.5	24.4	18.9	8.5	11.3	4.6	7.6	11.5	7.6	
MCZ 134392		37.0	26.0	20.0	9.5	13.0	4.8	8.6	12.2	7.9	
AGJR-T 504		38.0	26.4	20.7	9.0	12.4	4.8	8.0	11.4	7.6	
MCZ 134393		38.0	26.0	20.0		12.0	5.0	8.0	12.0	7.1	
MCZ 134396		38.0	25.0	19.0		11.6	4.4	8.0	11.0	7.3	
MCZ 142495		41.0	27.6	22.2	9.6	14.4	5.6	8.9	12.5	8.2	
AMNH 86547		46.0	34.0	27.8	10.6	14.2	5.6	9.8	15.5	8.4	
AMNH 86544		50.7	37.3	30.3	12.2	15.4	5.4	10.3	16.2	9.5	
<i>Chelodina pritchardi</i>											
AGJR-T 1608		32.2	20.8	18.0	7.6	9.8	3.3	7.5	10.6	4.8	
AGJR-T 1607		34.1	21.6	18.7	7.7	9.8	3.6	7.9	11.3	5.0	
AGJR-T 1606		35.5	22.8	19.8	8.3	10.5	4.1	8.4	12.1	5.1	
AGJR-T 1605		37.0	23.8	20.5	8.8	10.7	4.0	8.4	12.1	5.3	
AMNH 139735		39.5	26.5	21.5	8.8	11.0	4.5	8.5	13.6	5.7	
MCZ 175813		44.5	29.0	24.8	10.0	12.6	4.5	10.5	15.8	6.0	
<i>Chelodina reimanni</i>											
AGJR-T 1614		42.9	30.7	23.1	10.6	16.0	6.5	9.0	13.4	9.3	
AGJR-T 746		47.7	39.5	28.4	13.5	19.4	7.3	10.6	12.2	10.3	

TABLE 4. MEANS AND STANDARD DEVIATIONS FOR SKULL MEASUREMENT RATIOS OF FOUR *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 3.

Feature	<i>C. longicollis</i> (n = 7)	<i>C. pritchardi</i> (n = 6)	<i>C. novaeguineae</i> (n = 15)	<i>C. reimanni</i> (n = 2)
SWT/SL	.642 ± .014	.648 ± .013	.687 ± .024	.774 ± .076
SWM/SL	.501 ± .020	.553 ± .006	.532 ± .032	.568 ± .039
SD/SL	.260 ± .011	.290 ± .009	.320 ± .018	.388 ± .026
TW/SL	.119 ± .009	.144 ± .005	.194 ± .009	.218 ± .003
PtW/SWT	.521 ± .027	.522 ± .014	.461 ± .018	.372 ± .090
IOW/OW	.456 ± .052	.470 ± .037	.570 ± .055	.705 ± .024

not. This represents a major difference between the otherwise somewhat similar skulls of *C. pritchardi* and *C. longicollis*. The pterygoid trochlear processes are prominent and markedly divergent in *C. novaeguineae* and *C. reimanni*, with New Guinean specimens exhibiting prominent flaring, while Australian ones exhibit none; the processes are minimally divergent and much less prominent in *C. longicollis* and *C. pritchardi*. The ventral view of the skull shows the flared pterygoid processes are very prominent in New Guinean *C. novaeguineae* and *C. reimanni*, less prominent in the other species. Also, on the ventral view of the skull, the postorbital portions of the jugal and postorbital are well seen in *C. novaeguineae* and *C. reimanni*, but not in *C. longicollis* or *C. pritchardi*.

The parietal roof extent and shape differ markedly between the four species. *Chełodina reimanni* has an extremely narrow parietal crest, with nearly complete temporal emargination, *C. novaeguineae* also has an extremely narrow parietal crest, but with very slightly less emargination, *C. longicollis* has a fairly wide triangular parietal roof, with much less temporal emargination, and *C. pritchardi* is intermediate in both roof extent and temporal emargination. In *C. reimanni* the frontal enters the temporal emargination border, in *C. novaeguineae* and the other species it does not. The height of the supraoccipital crest above the foramen magnum is extremely high in *C. reimanni*, high in *C. novaeguineae*, low in *C. longicollis*, and intermediate in *C. pritchardi*. The volume of the temporal fossa (occupied by the mandibular ad-

ductor muscle mass) is extremely large in *C. reimanni*, large in *C. novaeguineae*, smaller in *C. longicollis*, and intermediate in *C. pritchardi*.

The lateral view of the skull reveals that the relative positions of the postorbital wall strut and of the anterior edge of the brain case differ in the four species. In *C. reimanni* and *C. novaeguineae* the postorbital wall is relatively caudad and overlaps the anterior brain case, giving increased stability and strength to the anterior third of the skull. In *C. longicollis* the postorbital wall is further cephalad, making it possible to look directly through the skull between the wall and the anterior brain case, and providing less strength and stability to the anterior skull. In *C. pritchardi* this relationship of the postorbital wall and the anterior edge of the brain case is intermediate.

All four species share the following skull osteological characteristics typical of other *Chelodina*: frontals fused, prefrontals separated by frontals, nasals present, dentaries sutured, splenials present, exoccipital contact above foramen magnum, temporal arch absent, and chelid foramen absent (variably present in rudimentary form in *C. longicollis*) (see McDowell, 1983; this "chelid foramen" is also called the posterior pterygoid foramen by Legler, personal communication).

Most of the differences in skull osteology reflect the increased robusticity of the skulls in *C. novaeguineae* and *C. reimanni*, with *C. longicollis* being the least robust, and *C. pritchardi* being intermediate. These differences can be calculated and demonstrated graphically as a Robusticity Index (RI; see Fig. 13). This Index reflects the cumulative effects of increased triturating surface width, overall tympanic skull width, and skull depth for adductor muscle volume, and is determined by the formula that follows.

$$RI = \frac{TW \times SWT \times SD}{SL}$$

In this formula, TW = maxillary triturating surface width, SWT = tympanic skull width, SD = midline skull depth, and SL = skull length. The Robusticity Index increases ontogenetically with size and age, and is significantly different in the four species. Increased robusticity is directly related to the increased width of

the maxillary and mandibular triturating surfaces and accompanying skeletal modifications of the skulls. These modifications reflect the secondary requirements for increased posterior skull bracing resistance and increased muscular mass to allow for increased mandibular muscle adductor force generation. These skeletal modifications have also created heavier and more massive skulls in the more robust species, which can additionally be demonstrated through an analysis of relative skull and mandible mass (grams per mm skull length) versus carapace length (Fig. 14), where *C. novaeguineae* and *C. reimanni* have heavier skulls than *C. longicollis*, and *C. pritchardi* is once again intermediate.

Based on skull osteology, *C. reimanni* and *C. novaeguineae* are probably dependent on a mollusciform and gastropod diet requiring extensive crushing of hard food matter. The diets of *C. longicollis* and *C. pritchardi* are probably more generalized carnivorous or piscivorous, with less dependence on hard-shelled bivalves and snails.

Some differences were noted between skulls of New Guinean versus Australian *C. novaeguineae*. However, full analysis of external morphological differences was not undertaken, and only a few Australian specimens were available for complete study. It is premature to evaluate whether these populations are distinct or not, and they are treated here as conspecific.

Cervical Spine. Central cervical articulation pattern is (2(3(4(5)6)7(8) in 5 specimens (4 by direct exam, 1 by X-ray), the only known pattern for all Chelidae as described by Williams (1950). Atlanto-axial (C1 and C2) cervical morphology is identical in all four species: *C. pritchardi*, *C. novaeguineae*, *C. reimanni*, and *C. longicollis*.

Shell. No neural bones in 7 specimens, all pleurals meeting in the midline. Axillary buttress moderately robust, articulating with lateral first pleural and posterior third peripheral, inguinal buttress less robust, articulating with postero-lateral edge of fourth and antero-lateral edge of fifth pleurals, and anterior seventh peripheral. Suprapygal relatively wide, contacting tenth peripheral. One specimen with atypical ten peripherals on each side, rather than normal eleven. Broad contact between first peripherals and first pleurals.

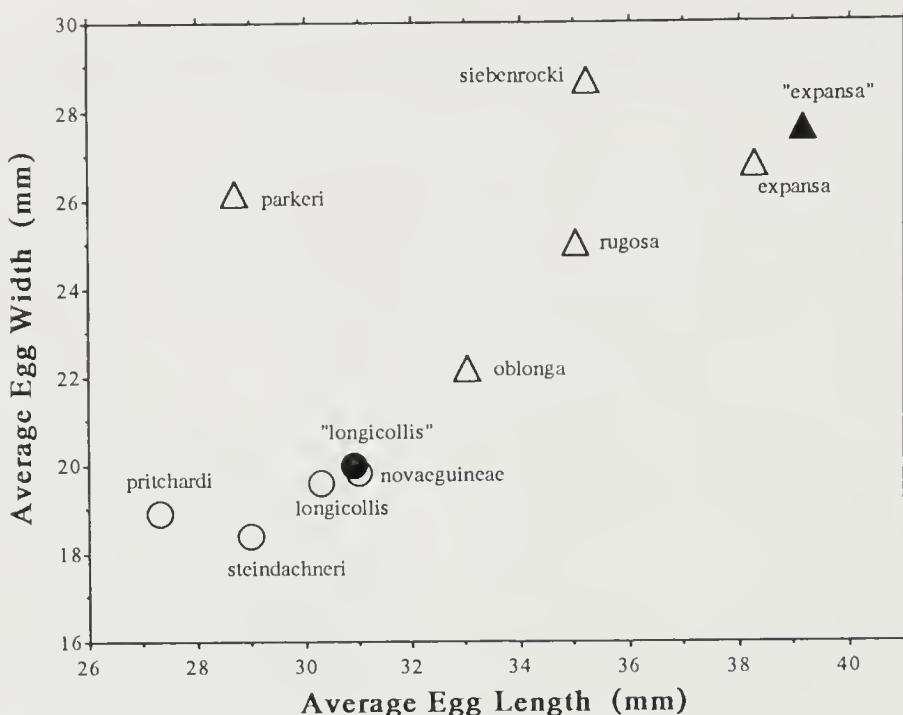


Figure 15. Plot of average egg width versus average egg length in all species of *Chelodina*. Circles represent subgeneric group "A" species; triangles, subgeneric group "B" species. Solid symbols are Legler's (1985) composite groups. See Table 5 for supporting data.

Ecology and General

Reproduction. Two specimens, obtained from Hula, each had eggs. The larger female (CL 228 mm) laid 4 eggs in captivity in Florida, one was broken, the other three measured 27.9 × 19.2, 27.8 × 18.0, and 27.0 × 18.6 mm. The smaller female (CL 193 mm) had one shelled oviducal egg measuring 26.4 × 19.7 mm when dissected post-mortem. All eggs were white, oval, with hard, brittle shells. Eggs are smaller than any other species of *Chelodina* (Table 5 and Fig. 15), but similar in shape to most other *Chelodina* (Fig. 16). Compared to the size of the adult female, the eggs laid by *C. pritchardi* are proportionately extremely small (Fig. 17).

Growth. The sub-adult male holotype has prominent concentric wide growth zones evident on carapacial and plastral scutes indicating rapid juvenile growth. No larger adults noted with similar growth evidence.

Sympatry. *Chelodina pritchardi* occurs sympatrically with *Emydura subglobosa* in the Kemp Welch River drainage basin. Both of these species are commonly eaten by the local inhabitants

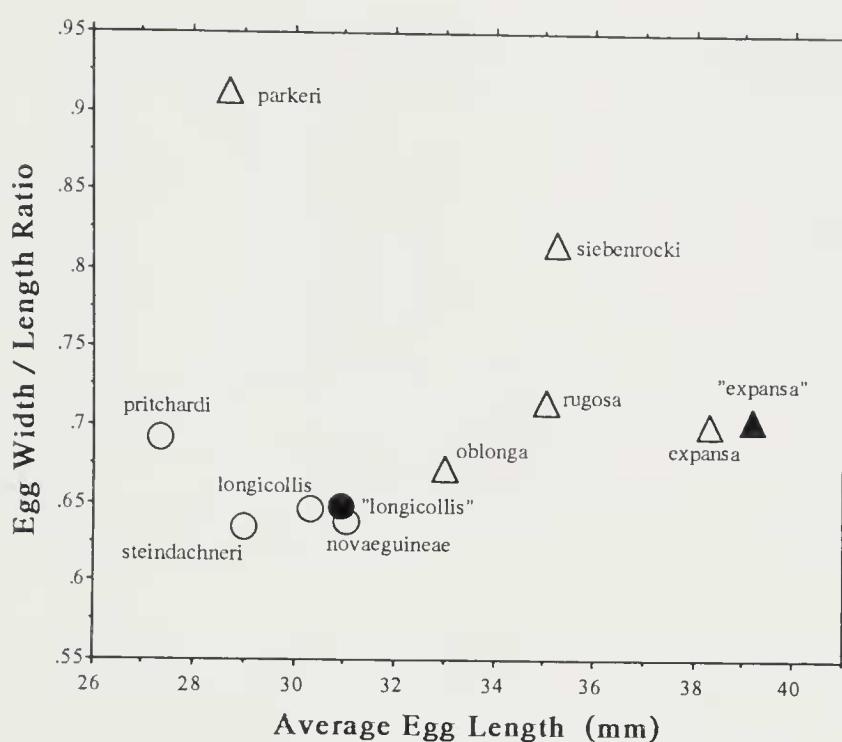


Figure 16. Plot of egg width/length ratio versus average egg length in all species of *Chelodina*. Circles represent subgeneric group "A" species; triangles, subgeneric group "B" species. Solid symbols are Legler's (1985) composite groups. See Table 5 for supporting data.

and often kept in the villages. The giant softshell turtle *Pelochelys bibroni* occurs in the Laloki River in the Port Moresby region and may be sympatric with *C. pritchardi*, which has tentatively been recorded from the same area.

Vernacular Names. In the inland regions of the Kemp Welch River area, the local language is Sinaugoro (Guise, 1985). All freshwater turtles are known as *gaokori*, but *C. pritchardi* and *E. subglobosa* do not have different names, despite the fact that the villagers readily distinguished them as being different. The Sinaugoro name for marine turtles is *gaogao*. In the coastal regions the local language is Keapara (Guise, 1985) and only one vernacular name, *aoao*, refers to both marine and freshwater swamp turtles (see also Rhodin *et al.*, 1980).

DISCUSSION

Chelodina pritchardi is in most ways more closely related to its geographically distant Australian congener *C. longicollis* than it is to the more geographically proximate New Guinean *C. novae-*

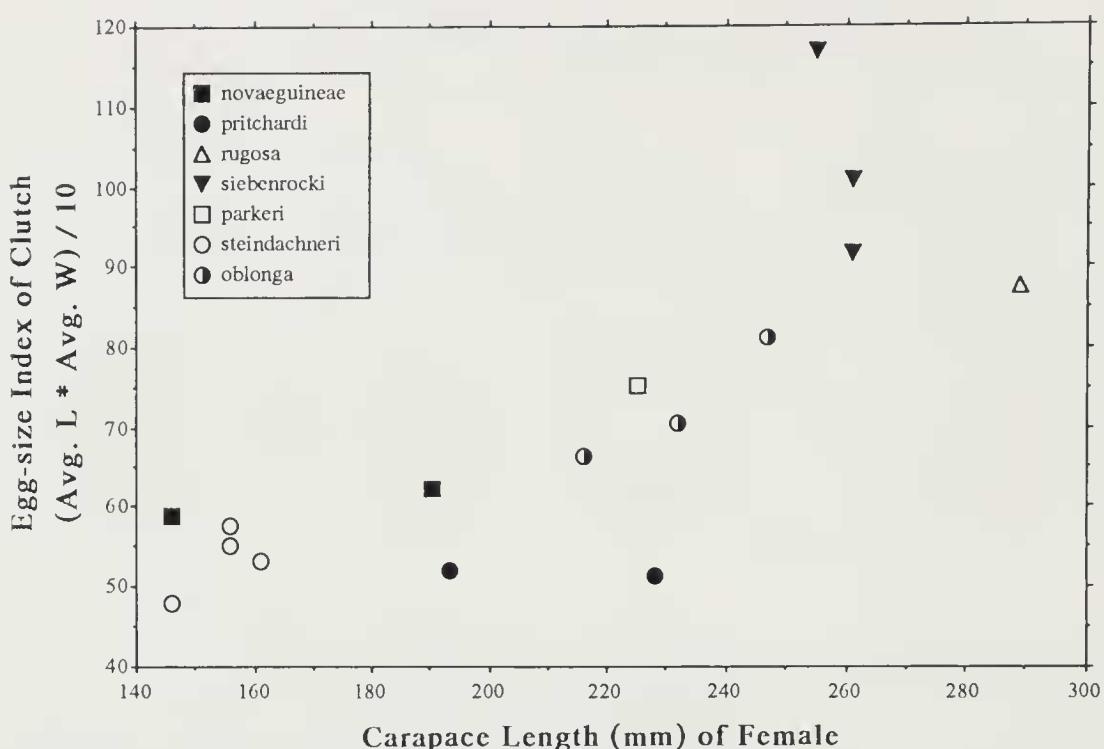


Figure 17. Plot of egg-size index of individual clutches (avg. egg length \times avg. egg width/10) versus carapace length of female that laid the clutch. Smaller index indicates smaller eggs. Data based on information from sources in Table 5. Note that for its body size, *C. pritchardi* has eggs relatively smaller than the other taxa.

guineae or *C. reimanni*. A number of shared osteological features of the skull suggest a close phylogenetic relationship between *C. pritchardi* and *C. longicollis*, and I regard them as more closely related to each other than either is to any other species. Superficially, however, based on only external morphology, *C. pritchardi* appears more similar to *C. novaeguineae* than to *C. longicollis*.

Chelodina novaeguineae is more similar to *C. pritchardi* than it is to *C. longicollis*, but its most closely related congener is *C. reimanni*. This latter species was described in 1990 by Philippen and Grossman, but they failed to describe the osteology or to compare their species to other New Guinean or Australian *Chelodina*. I have had an opportunity to examine several specimens of *C. reimanni*, including two osteological preparations (AGJR-T 746, a female of 199 mm carapace length from Merauke, Irian Jaya obtained via Michael Reimann and Walter Sachsse, and AGJR-T 1614, a female of 170.5 mm carapace length from Mer-

TABLE 5. AVERAGE LENGTH AND WIDTH OF EGGS FOR VARIOUS SPECIES OF *CHELODINA*. CL_{Max} = MAXIMUM CARAPACE LENGTH (MM). VALUES: MEAN ± STANDARD DEVIATION (RANGE) (MM). *CHELODINA "LONGICOLLIS"*, AND "*EXPANSA*" (IN QUOTATIONS) ARE THE SUBGENERIC GROUPINGS OF LEGLER, WHERE HE COMBINES DATA FROM SEVERAL DIFFERENT SPECIES.

Species	CL _{Max}	Eggs _n	Length	Width	Reference
<i>C. pritchardi</i>	228	4	27.3 ± 0.71 (26.4–27.9)	18.9 ± 0.74 (18.0–19.7)	Present study
<i>C. novaeguineae</i>	218	12	31.0 ± 1.08 (29.2–32.3)	19.8 ± 0.86 (18.5–20.9)	Present study
<i>C. siebenrocki</i>	290	64	35.2 ± 1.70 (31.6–38.3)	28.7 ± 1.10 (27.2–31.7)	Rhodin and McCord, 1990; Rhodin and Mittermeier, 1976
<i>C. parkeri</i>	267	13	28.7 ± 3.20 (25.5–32.0)	26.2 ± 0.80 (24.0–27.0)	Ewert, 1985; Fritz and Jauch, 1989
<i>C. oblonga</i>	247	80	33.0 ± 1.30 (30.8–35.7)	22.2 ± 1.57 (18.1–24.0)	Clay, 1981; Kuchling, 1988
<i>C. rugosa</i>	304	14	35.0	25.0	Cann, 1978
<i>C. expansa</i>	375	46	38.3 ± 0.30 (33.5–41.9)	26.8 ± 0.40 (22.2–30.1)	Georges, 1986
<i>C. "expansa"</i>	375	304	39.2 ± 3.40 (30.7–46.9)	27.6 ± 2.41 (19.5–31.0)	Legler, 1985
<i>C. steindachneri</i>	193	30	29.0 ± 0.94 (27.5–31.0)	18.4 ± 0.80 (17.0–19.5)	Kuchling, 1988
<i>C. longicollis</i>	240	154	30.3 ± 0.83 (21.0–33.8)	19.6 ± 0.27 (12.5–21.3)	Vestjens, 1969; Legler and Cann, 1980
<i>C. longicollis</i>	240	169	31.2 ± 0.1	20.2 ± 0.1	Palmer-Allen <i>et al.</i> , 1991
<i>C. "longicollis"</i>	279	282	30.9 ± 2.88 (20.2–42.5)	20.0 ± 1.86 (15.8–29.1)	Legler, 1985

auke obtained via Frank Yowono and William McCord). *Chelodina reimanni* is most similar to *C. novaeguineae* and the features of increased skull robusticity seen in *C. novaeguineae* are further amplified in *C. reimanni*. Its skull is massively enlarged and heavy, with wide triturating surfaces, a narrow parietal crest, large temporal fossa, and increased buttressing in a deep, wide skull. It has small fused premaxillas and lacks chelid foramina. I regard *C. novaeguineae* and *C. reimanni* as more closely related to each other than either is to any other species, and from my preliminary examination, I also recognize *C. reimanni* as being distinct from *C. novaeguineae*.

Phylogenetically, I consider enlarged maxillary and mandibular triturating surfaces and increased skull robusticity as derived features within the *Chelodina* lineage. Though clearly diet-related, these features represent a significant specialization by only a few members of the genus, notably *C. reimanni* and *C. novaeguineae*. These shared derived characteristics suggest a close phylogenetic relationship between these two species. The narrow triturating surfaces and less robust skulls of *C. pritchardi* and *C. longicollis* represent more primitive features within the genus and suggest retained plesiomorphic features in those two species. These primitive features are also present in the only other member of *Chelodina* subgeneric group "A", the western Australian species *C. steindachneri*. Examination of skulls of this species demonstrates that it is most similar to *C. longicollis*, with narrow triturating surfaces, a relatively wide anterior parietal roof, shallow temporal fossa, and markedly decreased skull robusticity. Unlike *C. longicollis*, however, it usually retains fairly well-formed chelid foramina (posterior pterygoid foramen of Legler), a relatively primitive feature among all *Chelodina*. The chelid foramen is absent in all other members of *Chelodina* subgeneric groups "B" and "A" except for *C. longicollis*, where it is variably present but usually absent.

Of the five currently recognized taxa in *Chelodina* subgeneric group "A", I regard *C. reimanni* as the most derived, and *C. steindachneri* as the most primitive. The other three species fall out in a series between these extremes, with *C. novaeguineae* most derived, *C. longicollis* most primitive, and *C. pritchardi* intermediate between the two. Two alternate phylogenetic hypotheses

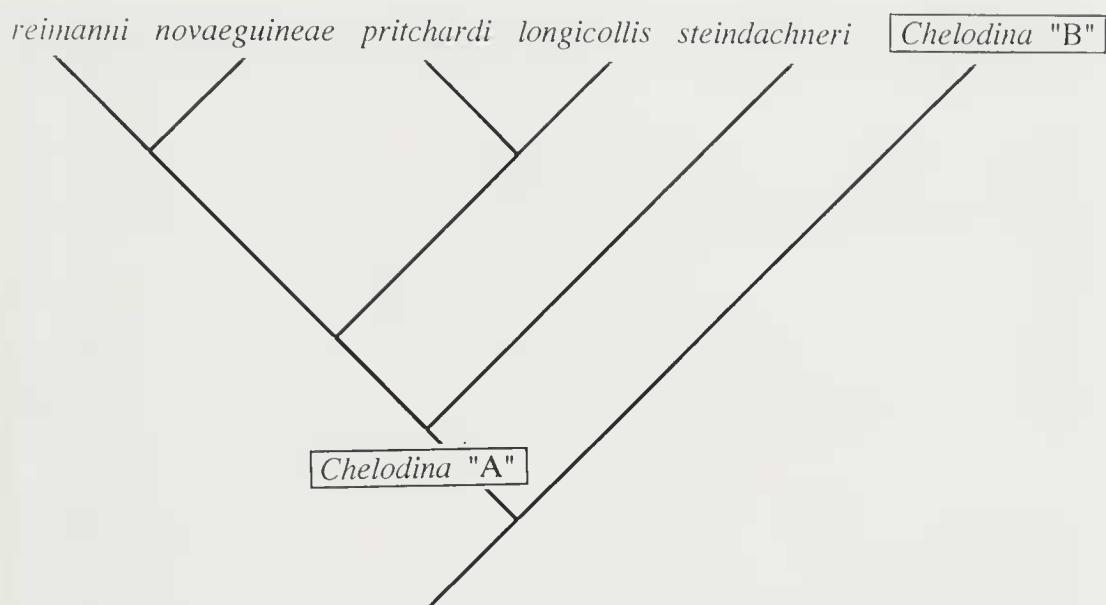


Figure 18. Hypothesized relationships of the currently recognized species of *Chełodina* subgeneric group "A". See Figure 19 for an alternative phylogenetic hypothesis.

expressing the possible relationships within *Chełodina* subgeneric group "A" are depicted in Figures 18 and 19, with Figure 18 representing what I consider the more likely hypothesis. This hypothesis would be strengthened through the discovery of shared

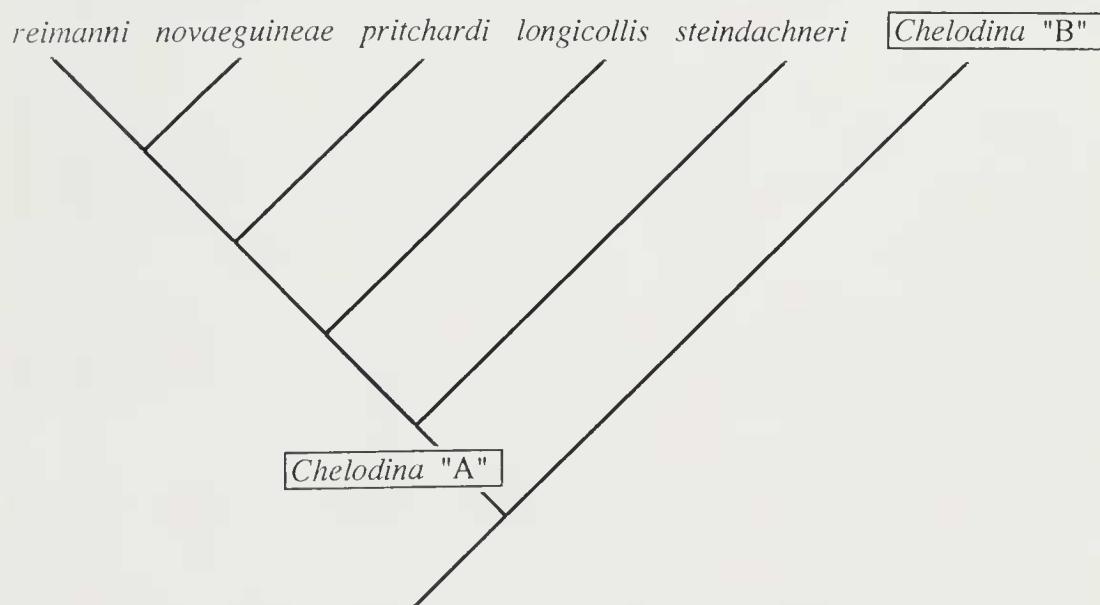


Figure 19. Alternative phylogenetic relationships of *Chełodina* subgeneric group "A". See Figure 11 for preferred hypothesis.

derived features between *C. pritchardi* and *C. longicollis*, and is encumbered by the less parsimonious double loss of chelid foramina in the *novaeguineae-reimanni* lineage and the *pritchardi-longicollis* clade. Clearly, a rigorous cladistic analysis of multiple morphologic features of all the species of *Chelodina* will be necessary to help further elucidate the phylogenetic history of the genus.

These five taxa of *Chelodina* subgeneric group "A" form a well-defined monophyletic assemblage clearly differentiated from *Chelodina* subgeneric group "B". Features of shell morphology, head width, skull osteology, and cervical spine length and morphology clearly define the two groups. The currently recognized genus *Chelodina* (sensu lato) is also a clearly defined monophyletic assemblage with a long list of shared derived characteristics (see Gaffney, 1977). Recognition of this monophyly needs to be incorporated into whatever taxonomic arrangement provides the most specific nomenclatorial definition of the subgroups involved. Whether the "subgeneric" groups "A" and "B" are best recognized as subgenera of *Chelodina* or as full separate genera awaits full evaluation by Legler (in preparation). My own analysis of the phylogenetic relationships of all the Chelidae of Australasia and South America (in preparation) suggests recognition at the generic level for these two separate groups of *Chelodina*, with a new suprageneric category replacing our old concept of *Chelodina*.

ACKNOWLEDGMENTS

I thank Peter C. H. Pritchard for his donation of the two specimens which stimulated this study and William P. McCord for his generosity in allowing me to examine and measure his large series of live captive animals. I also thank Richard Zweifel, opportunely present in Papua New Guinea when I collected the holotype, for facilitating export of the specimen via the American Museum of Natural History to the MCZ. Susan and Michael Rhodin provided valuable field assistance and José Rosado at the MCZ curated specimens and helped with logistics. I prepared all illustrations. For the loan of other study specimens and general assistance with the project, I also thank John Legler, Robert Winokur, Arnold Kluge, Allen Greer, Ron Heyer, Sam McDowell, Alan Leviton, A. F. Stimson, Philip Hall, Walter Sachsse, Chuck

Crumly, John Iverson, John Carr, Russ Mittermeier, and Ernest Williams.

APPENDIX

Comparative material examined; collection acronyms as follows: AGJR-T = personal collection of Rhodin (including preserved specimens, voucher photographs, and reliably documented database entries, including data from many live specimens measured in the unnumbered personal collection of William P. McCord); AMNH = American Museum of Natural History; AMS = Australian Museum, Sydney; BMNH = British Museum of Natural History; CAS = California Academy of Sciences; FMNH = Field Museum of Natural History; MCZ = Museum of Comparative Zoology; MTKD = Museum für Tierkunde, Dresden; PCHP = personal collection of Peter C. H. Pritchard; PNGM = Papua New Guinea Museum; SMcD = collection of Samuel McDowell; UMMZ = University of Michigan Museum of Zoology; UNLV = University of Nevada, Las Vegas; USNM = United States National Museum; UU = University of Utah.

Chelodina longicollis: **Australia:** New South Wales: Armidale (nr.), UNLV s/n (15); Sydney, AMNH 14151; Sydney, 60 mi S, UMMZ 130161, 130549; Talbnager R., 8 mi W Varbry, btw. Dunedo and Cassilis, AMS 40828; Victoria: Bright, FMNH 75317; Patho, 5 mi S Murray R., 20 mi W Echuca, UU s/n, AMNH 108952, Queensland: Burnett R., FMNH 16885; Capella, 20 mi W, CAS 77809; Duaringa, 15 mi S, CAS 77808; Eidsvold, upper Burnett River, AMS 5979; No data: AMNH s/n (2), UU s/n, AGJR-T 133, 158-9, 179, AMNH 2323, MCZ 8369, 8371-7, 86783-4, USNM 8894, AMNH 9002, 45079, 45085, 75165, 97629, 110483, MTKD 14605, FMNH 22681, 31047, 35538, BMNH 1947.3.5.86 (holotype of *C. longicollis*), BMNH 1947.3.5.87 (holotype of *C. sulcata*).

Chelodina novaeguineae: **Australia:** Queensland: Alice River, 15 mi WSW Townsville, UMMZ 132328; Armarynald, 26 mi SE Burketown, AMNH 86545-7, Burdekin River, lower, BMNH 1908.2.25.1; Edward River, Cape York, UU 14718; Greta Creek, PCHP 2385; Staaten R., 100 mi. N Normanton, AMNH 86543-4; Northern Territory: Batten Creek, 13 mi WSW Borroloola, UU 14716; Indonesia: Irian Jaya: Kuprik, nr. Merauke ($8^{\circ}25'S$, $140^{\circ}28'E$), SMcD 49-1, 49-2; Papua New Guinea: Western Province: Abam, Oriomo R. ($8^{\circ}57'S$, $143^{\circ}13'E$), AMNH 117939, MCZ 120353, 127404, 134390-1, 134709-10, 134712; Ali Village, Aramia River ($8^{\circ}05'S$, $142^{\circ}55'E$), USNM 213490; Boze, Binaturi River ($9^{\circ}05'S$, $143^{\circ}01'E$), AGJR-T 504; Daru Roads ($9^{\circ}03'S$, $143^{\circ}12'E$), MCZ 142500; Emeti, Bamu River ($7^{\circ}48'S$, $143^{\circ}15'E$), MCZ 138102; Fly River at Strickland River junction ($7^{\circ}35'S$, $141^{\circ}25'E$), MCZ 53758-61; Giringaredé, Binaturi River ($9^{\circ}03'S$, $142^{\circ}57'E$), MCZ 153930; Katatai ($9^{\circ}01'S$, $143^{\circ}18'E$), MCZ 138101, 142495, 154340;

Katow (= Mawatta, Binaturi River) (9°08'S, 142°55'E), BMNH 1946.1.22.36 (lectotype *C. novaeguineae*); Komovai Village, Fly River (7°33'S, 141°15'E) AGJR-T 1338; Kuru, Binaturi River (8°55'S, 143°04'E), MCZ 134711; Lake Daviumbo (7°35'S, 141°17'E), AMNH 59874; Lake Murray (7°00'S, 141°30'E), MCZ 134392; Mabaduane, Pahoturi River (9°17'S, 142°44'E), AMNH 57589-91, MCZ 137516; Masingle, Binaturi River (9°07'S, 142°55'E), AGJR-T 501, MCZ 153046-8, 153906, 153923, 153926; Morehead (8°43'S, 141°38'E), PNGM 23505; No data, USNM 231527; Oriomo, Oriomo River (8°52'S, 143°10'E), PNGM 23510; Peawa, Oriomo River (8°55'S, 143°12'E), AMNH 104010; Tarara, Wassikussa River (8°50'S, 141°52'E), AMNH 58410; Togo, Pahoturi River (9°14'S, 142°40'E), PNGM 23502-3, 23511, MCZ 134393-6; Ume, Binaturi River (9°03'S, 143°03E), PNGM 22407, MCZ 127405; Wipim (8°51'S, 142°55'E), USNM 204856.

Chelodina pritchardi: Papua New Guinea: Central Province: Bore, Kemp Welch River (9°53'S, 147°46'E), MCZ 173543; nr. Hula, Kemp Welch River basin (10°06'S, 147°43'E), MCZ 175813, AMNH 139735; nr. Port Moresby, PNGM 23373; ca. 10 km east of Bore, Kemp Welch River, AGJR-T 1575-1609, 1643-6.

Chelodina reimanni: Indonesia: Irian Jaya: Merauke (8°25'S, 140°28'E), AGJR-T 746, 1299-1300, 1325, 1614-1619, 1642; No data: MTKD 14603.

Chelodina steindachneri: Australia: Western Australia: Marloo Station, MCZ 33501; Mundabullangana, MCZ 74871, 134469; 1 mi S. Minilya River on NW coastal hwy., MCZ 74872; Woodstock, AMNH 101977-9.

LITERATURE CITED

BOULENGER, G. A. 1888. On the chelydoid chelonians of New Guinea. Annali del Museo Civico di Storia Naturale di Genova, (2a)6: 449-452.

BOULENGER, G. A. 1889. Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History). London, Trustees of the Museum. 311 pp.

BURBIDGE, A. A., J. A. W. KIRSCH, AND A. R. MAIN. 1974. Relationships within the Chelidae (Testudines: Pleurodira) of Australia and New Guinea. Copeia, 1974: 392-409.

CANN, J. 1978. Tortoises of Australia. Sydney, Angus and Robertson. 79 pp.

CLAY, B. T. 1981. Observations on the breeding biology and behaviour of the long-necked tortoise, *Chelodina oblonga*. Journal of the Royal Society of Western Australia, 64: 27-32.

EWERT, M. A. 1985. Embryology of turtles, pp. 75-267. In C. Gans, F. Billett, and P. F. A. Maderson (eds.), Biology of the Reptilia. London, Academic Press, Vol. 14.

FRITZ, U. AND D. JAUCH. 1989. Haltung, Balzverhalten und Nachzucht von Parkers Schlangenhalsschildkröte *Chelodina parkeri* Rhodin & Mittermeier, 1976 (Testudines: Chelidae). Salamandra, 25(1): 1-13.

GAFFNEY, E. S. 1977. The side-necked turtle family Chelidae: A theory of relationships using shared derived characters. American Museum Novitates, 2620: 1-28.

GEORGES, A. 1986. Observations on the nesting and natural incubation of the

long-necked tortoise *Chelodina expansa* in south-east Queensland. Herpetofauna, **15**(2): 27–31.

GIBBONS, J. W. AND J. E. LOVICH. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). Herpetological Monographs, **4**: 1–29.

GOODE, J. 1967. Freshwater Tortoises of Australia and New Guinea (in the Family Chelidae). Melbourne, Lansdowne Press. 154 pp.

GUISE, A. 1985. Oral tradition and archaeological sites in the eastern Central Province. Papua New Guinea National Museum Records, **9**: 1–84.

ICZN. 1991. Decision of the Commission. Three works by Richard W. Wells and C. Ross Wellington: proposed suppression for nomenclatural purposes. Bulletin of Zoological Nomenclature, **48**(4): 337–338.

KING, F. W. AND R. L. BURKE. 1989. Crocodilian, Tuatara, and Turtle Species of the World. A Taxonomic and Geographic Reference. Washington, DC, Association of Systematics Collections. 216 pp.

KUCHLING, G. 1988. Gonadal cycles of the Western Australian long-necked turtles *Chelodina oblonga* and *Chelodina steindachneri* (Chelonia: Chelidae). Records of the Western Australian Museum, **14**: 189–198.

LEGLER, J. M. 1985. Australian chelid turtles: reproductive patterns in wide-ranging taxa, pp. 117–123. In G. Grigg, R. Shine, and H. Ehmann (eds.), Biology of Australasian Frogs and Reptiles. Royal Zoological Society of New South Wales. 527 pp.

LEGLER, J. M. AND J. CANN. 1980. A new genus and species of chelid turtle from Queensland, Australia. Contributions in Science of the Natural History Museum of Los Angeles County, **324**:1–18.

MCDOWELL, S. B. 1983. The genus *Emydura* (Testudines: Chelidae) in New Guinea with notes on the penial morphology of Pleurodira, pp. 169–189. In A. G. J. Rhodin and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. Cambridge, Massachusetts, Museum of Comparative Zoology. 725 pp.

PALMER-ALLEN, M., F. BEYNON, AND A. GEORGES. 1991. Hatchling sex ratios are independent of temperature in field nests of the long-necked turtle, *Chelodina longicollis* (Testudinata: Chelidae). Wildlife Research, **18**: 225–231.

PHILIPPEN, H.-D. AND P. GROSSMAN. 1990. Eine neue Schlangenhalschildkröte von Neuguinea: *Chelodina reimanni* sp. n. (Reptilia, Testudines, Pleurodira: Chelidae). Zoologische Abhandlungen, Staatliches Museum für Tierkunde, Dresden, **46**(5): 95–102.

RHODIN, A. G. J. AND W. P. MCCORD. 1990. Reproductive data on the chelid turtle *Chelodina siebenrocki* from New Guinea. Herpetological Review, **21**(3): 51–52.

RHODIN, A. G. J. AND R. A. MITTERMEIER. 1976. *Chelodina parkeri*, a new species of chelid turtle from New Guinea, with a discussion of *Chelodina siebenrocki* Werner, 1901. Bulletin of the Museum of Comparative Zoology, **147**(11): 465–488.

RHODIN, A. G. J., S. SPRING, AND P. C. H. PRITCHARD. 1980. Glossary of turtle vernacular names used in the New Guinea region. Journal of the Polynesian Society, **89**(1): 105–117.

SHAW, G. 1794. Zoology of New Holland. Vol. I. London, J. Davis. 33 pp.

SIEBENROCK, F. 1914. Eine neue *Chelodina* Art aus Westaustralien. Anzeiger der Akademischen Wissenschaften Wien, **17**: 386–387.

VESTJENS, W. J. M. 1969. Nesting, egg-laying and hatching of the snake-necked tortoise at Canberra, A.C.T. Australian Zoology, **15**(2): 141–149.

WELLS, R. W. AND C. R. WELLINGTON. 1985. A classification of the Amphibia and Reptilia of Australia. Australian Journal of Herpetology, Supplemental Series, **1**: 1–61.

WERNER, F. 1901. Ueber Reptilien und Batrachier aus Ecuador und Neu-Guinea. Verhandlungen der Zoologisch-Botanischen Gesellschaft Wien, **51**: 593–603.

WILLIAMS, E. E. 1950. Variation and selection in the cervical central articulations of living turtles. Bulletin of the American Museum of Natural History, **94**: 510–561.